# TENTACULARIID CESTODES OF THE ORDER TRYPANORHYNCHA (PLATYHELMINTHES) FROM THE AUSTRALIAN REGION

H. W. PALM & I. BEVERIDGE

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The present study summarises information on tentaculariid trypanorhynchs from Australian waters. A total of 19 species from the genera *Nybelinia* Poche, 1926, *Heteronybelinia* Palm, 1999, *Mixonybelinia* Palm, 1999, *Kotorella* Euzet & Radujkovic, 1989 and *Kotorelliella* gen. nov. were identified: *N. aequidentata* (Shipley & Hornell, 1906); *Nybelinia africana* Dollfus, 1960; *N. hemipristis* sp. nov.; *N. jayapaulazariahi* Reimer, 1980; *N. mehlhorni* sp. nov.; *N. schmidti* Palm, 1999; *N. scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996); *N. strongyla* Dollfus, 1960; *N. thyrsites* Korotaeva, 1971; *N. victoriae* sp. nov.; *Heteronybelinia australis* sp. nov.; *H. estigmena* (Dollfus, 1960); *H. pseudorobusta* sp. nov.; *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997); *M. cribbi* sp. nov.; *M. edwinlintoni* (Dollfus, 1960); *M. southwelli* Palm & Walter, 1999; *Kotorella pronosoma* (Stossich, 1901) and *Kotorelliella jonesi* gen. et sp. nov. The new genus *Kotorelliella* is characterised by a homeoacanthous, heteromorphous metabasal armature and a basal armature with additional interpolated hooks on the external surface of the tentacle, thus appearing heteroacanthous. The new species appears to be closely related to *Kotorella pronosoma*. The tentaculariid trypanorhynch fauna in Australian waters is species rich, with 22 (48%) of the total of 46 known species occurring in waters of the region. Eleven new locality, and 20 new host records are reported.

H. W. Palm, Institut für Zoomorphologie, Zellbiologie und Parasitologie, Heinrich-Heine-Universität Düsseldorf, Universitätsstraße 1, D-40225 Düsseldorf, Germany, current address: Centre for Coastal and Marine Resource Studies, Faculty of Fisheries and Marine Sciences, Bogor Agricultural University, 16680 Bogor, Indonesia; email: hpalm@indo.net.id, hpalm@gmx.net, and I. Beveridge, Department of Veterinary Science, University of Melbourne, Parkville, Victoria 3052, Australia. Manuscript received 20 November 2000.

Palm (1999), Palm et al. (1997), Palm and Overstreet (2000) and Palm and Walter (1999, 2000) partially revised the trypanorhynch cestode family Tentaculariidae Poche, 1926 on the basis of material deposited in museums in London, Paris, Vienna and the United States. Following the erection of two new genera, *Heteronybelinia* Palm, 1999 and *Mixonybelinia* Palm, 1999 by Palm (1999), Palm and Walter (2000) gave a summary of the current state of knowledge within the tentaculariid trypanorhynch genera. Thus, to date, a total of 39 species of *Kotorella*, *Nybelinia*, *Heteronybelinia* and *Mixonybelinia* are considered valid (Palm & Walter 2000).

There is little known about the tentaculariid trypanorhynchs from Australian coastal waters. The first collections were made by a French scientific expedition under the command of Nicolas Baudin between 1801 and 1803 (Beveridge & Campbell 1996), but the cestodes, *Tentacularia coryphaenae* Bosc, 1797 and an unidentified species of *Nybelinia* were not described until 1942 (Dollfus 1942). Korotaeva (1971) named the *Nybelinia* species of Dollfus (1942) *N. thyrsites* and subsequently (Korotaeva 1974) reported additional unidentified *Nybelinia* spp. from other fishes from southern Australia. Lester et al. (1988) and Sewell and Lester (1988) reported *Tentacularia* sp. from orange roughy, *Hoplostethus atlanticus* Collett, 1889 off the coasts of South Australia and Tasmania; while Sewell and Lester (1995) found *Nybelinia* sp. in jewfish, *Rexea solandri* (Cuvier & Valenciennes, 1832) from southern Australian waters. Beveridge and Campbell (1996) recorded *Tentacularia coryphaenae* Bosc, 1797, *Nybelinia thyrsites* Korotaeva, 1971 and *N. sphyrnae* Yamaguti, 1952 from Australian fishes; while Jones and Beveridge (1998) added *N. queenslandensis* from a carcharhinid shark as a new species. Palm (1999) recorded *Nybelinia lingualis* (Cuvier, 1817) from southern Australian waters and Speare (1999) reported Nybelinia sp. from sailfish, *Istiophorus platypterus* (Shaw & Nodder, 1792) off the coast of Queensland. Thus, a total of five tentaculariid species has been described from Australia.

Last and Stevens (1994) summarised knowledge of the Australian chondrichthyan fauna, the definitive hosts of trypanorhynchan cestodes, as being extremely rich and consisting of 296 species, 54% of them endemic. In terms of host-specificity and zoogeography of trypanorhynch cestodes, the Australian fauna might therefore harbour a high number of endemic and locally distributed tentaculariid trypanorhynchs, such as was observed within the related family Eutetrarhynchidae by Beveridge (1990). Palm (1999) and Palm and Walter (2000) suggested that many tentaculariids, for example *Tentacularia coryphaenae* and *Nybelinia lingualis*, exhibit a cosmopolitan or circumtropical distribution pattern. However, records from the south-west Pacific and south-east Indian Ocean are scarce. For example, the tentaculariids *Tentacularia coryphaenae*, *Nybelinia africana* and *N. scoliodoni* were only recently recorded from Indonesian coastal waters (Palm 2000). Other records which might confirm a wide distribution and possibly a low degree of host specificity for these trypanorhynchs are still lacking.

The present study was carried out to examine the species of *Nybelinia*, *Heteronybelinia*, *Mixonybelinia* and *Kotorella* deposited in museum collections in Australia as well as in the collection of the junior author. Where necessary, the specimens are described and illustrated as emendations to currently available descriptions. Apart from the establishment of new host and locality records, species identifications provide further insight into the zoogeographical distribution of tentaculariid cestodes. The comparison of the specimens with earlier descriptions allows comments to be made on the extent of intraspecific morphological variability within tentaculariid trypanorhynchs. Together with the study of deposited tentaculariids from other collections (Palm 1999; Palm & Overstreet 2000; Palm and Walter 1999, 2000), the present study summarises the current state of knowledge on the genera of tentaculariid cestodes.

## Material And Methods

Specimens were examined from the Australian Helminthological Collection (AHC) housed in the South Australian Museum (SAM), Adelaide, as well as the Queensland Museum (QM), Brisbane. Special attention was given to unidentified specimens deposited simply as *Nybelinia* sp. Unmounted specimens were stained in Celestine Blue, dehydrated in ethanol, cleared in methyl salicylate and mounted in Canada balsam. Pieces of strobilae were embedded in paraffin, serial sections were cut at a thickness of 5 µm and stained with haematoxylin and eosin. Drawings were made using an Olympus BH2 microscope with an ocular micrometer and drawing tube. Terminology for morphological features peculiar to the Trypanorhyncha follows Dollfus (1942) and Campbell and Beveridge (1994).

The following measurements were made: scolex length (SL), scolex width at level of pars bothridialis (SW), pars bothridialis (pbo), pars vaginalis (pv), pars bulbosa (pb), pars postbulbosa (ppb), velum (vel), appendix (app), bulb length (BL), bulb width (BW), bulb ratio (BR), scolex proportions of pbo:pv:pb (SP), tentacle width (TW) and tentacle sheath width (TSW). If possible, the tentacle length (TL) was estimated. The tentacular armature was described as follows: armature homeomorphous or heteromorphous, number of hooks per half spiral row (hsr), total hook length (L) and the total length of the base of the hooks (B). The abbreviation 'nm' (not measured) indicates that no measurement was taken. All measurements are given in micrometers unless otherwise indicated. Specimens belonging to the same species from different hosts or localities were measured in the same order as cited in the material examined. If more than three measurements were taken from a single host species, the mean is given with the range in parentheses. Because tentaculariid cestodes are morphologically uniform and the genera are well defined, the species descriptions presented here are restricted to key differential features. Illustrations are provided if useful for future species identification; otherwise the reader is referred to illustrations given by other authors. The classification utilised follows Palm (1995, 1997). Host identity follows Last and Stevens (1994) for the elasmobranchs and FishBase 1998 (Froese & Pauly 1998) for the teleosts.

## Systematics

A total of 19 species were identified, and 11 new locality and 20 new host records were established. Seven new species are described and a new tentaculariid genus is erected: *Nybelinia hemipristis* sp. nov., *N. mehlhorni* sp. nov., *N. victoriae* sp. nov., *Heteronybelinia australis* sp. nov., *H. pseudorobusta* sp. nov., *Mixonybelinia cribbi* sp. nov. and *Kotorelliella jonesi* gen. et sp. nov. Detailed information on individual specimens with comments on their taxonomy and distribution are provided below.

Order TRYPANORHYNCHA Diesing, 1863

Superfamily TENTACULARIOIDEA Poche, 1926

Family TENTACULARIIDAE Poche, 1926

## Genus *Nybelinia* Poche, 1926

***Nybelinia aequidentata*** Shipley & Hornell, 1906 (Figs 1–2)

*Material examined*

From *Dendrochirus zebra* (Cuvier, 1829): 1 postlarva, Noumea, New Caledonia, Nov. 1997, coll. S. Pichelin (QM G 218031).

*Description*

SL = 7900 (Fig. 1); SW = 1775; pbo = 2975; pv = 4950; pb = 1575; vel = 925; app = 1400; BL = 1417 (1400–1450); BW = 280 (270–290); BR = 5.1:1; SP = 1.9:3.1:1. Basal tentacular swelling absent. TW basal = 100–110, TW metabasal = 110–120. Tentacle sheaths straight, TSW = 80–100, prebulbar organs and muscular rings around basal part of tentacle sheaths not visible. Retractor muscles originate in basal parts of bulbs. Tentacular armature homeoacanthous, homeomorphous (Fig. 2); distinctive basal armature absent. Hooks falciform, with slender shaft, stout base and strongly recurved tip, L = 57.5–65.0; B = 17.7–22.5. Hooks decrease in size towards apical region and towards base L = 35.0–57.5; B = 12.5–17.5. Smallest hook measured L = 17.5; hsr = 7–8.

*Remarks*

The present specimen has one of the largest scoleces among *Nybelinia* species. In addition, the postlarva is characterised by falciform hooks over 60 in length and a bulb ratio greater than 4. The postlarva is most similar to *Nybelinia aequidentata* Shipley & Hornell, 1906, described by Shipley and Hornell (1906), Pintner (1927) and Palm (1999). Shipley and Hornell (1906) recorded the type specimen as having a scolex 4–5 mm long. The hook shape of the present specimen corresponds with those of the type, though the hooks in the present specimen are larger (57–65 compared with 49 in the type according to Shipley and Hornell (1906) or 33–38 reported by Palm (1999). Pintner (1927) redescribed the type and added information on the bulb ratio (4.3:1), hook length (48) and scolex measurements (SW = 1900, pbo = 1500, pb = 1600 and vel = 600). He also remarked that the hooks were not uniform in size but increased from the base towards the metabasal region and then decreased in the apical region of the armature. Thus, although the scolex and hook sizes of the present specimen are distinctly larger than those described from the type specimen, it has been identified as *N. aequidentata*. The present finding represents a new host and locality record.

*Nybelinia syngenes* Pintner, 1929 is the only other species of *Nybelinia* which has been described as having tentacular hooks with a length greater than 60 and with a similar hook form and armature pattern. However, the scolex of this species, described originally from *Sphyrna zygaena* (Linnaeus, 1758), is distinctly smaller. Whether *N. aequidentata* exhibits variation in scolex size, as described for *N. lingualis* (Cuvier, 1817) and *Heteronybelinia yamaguti* (Dollfus, 1960) (see Dollfus 1942; Palm et al. 1997; Palm 1999; Palm & Walter 2000) is not known. Palm (1999) has suggested that this might be the case for a postlarva from *Lepturacanthus savala* (Cuvier, 1829) with a scolex length of 3400, a bulb ratio of 3.3:1 and slender falciform hooks 33–38 in length.

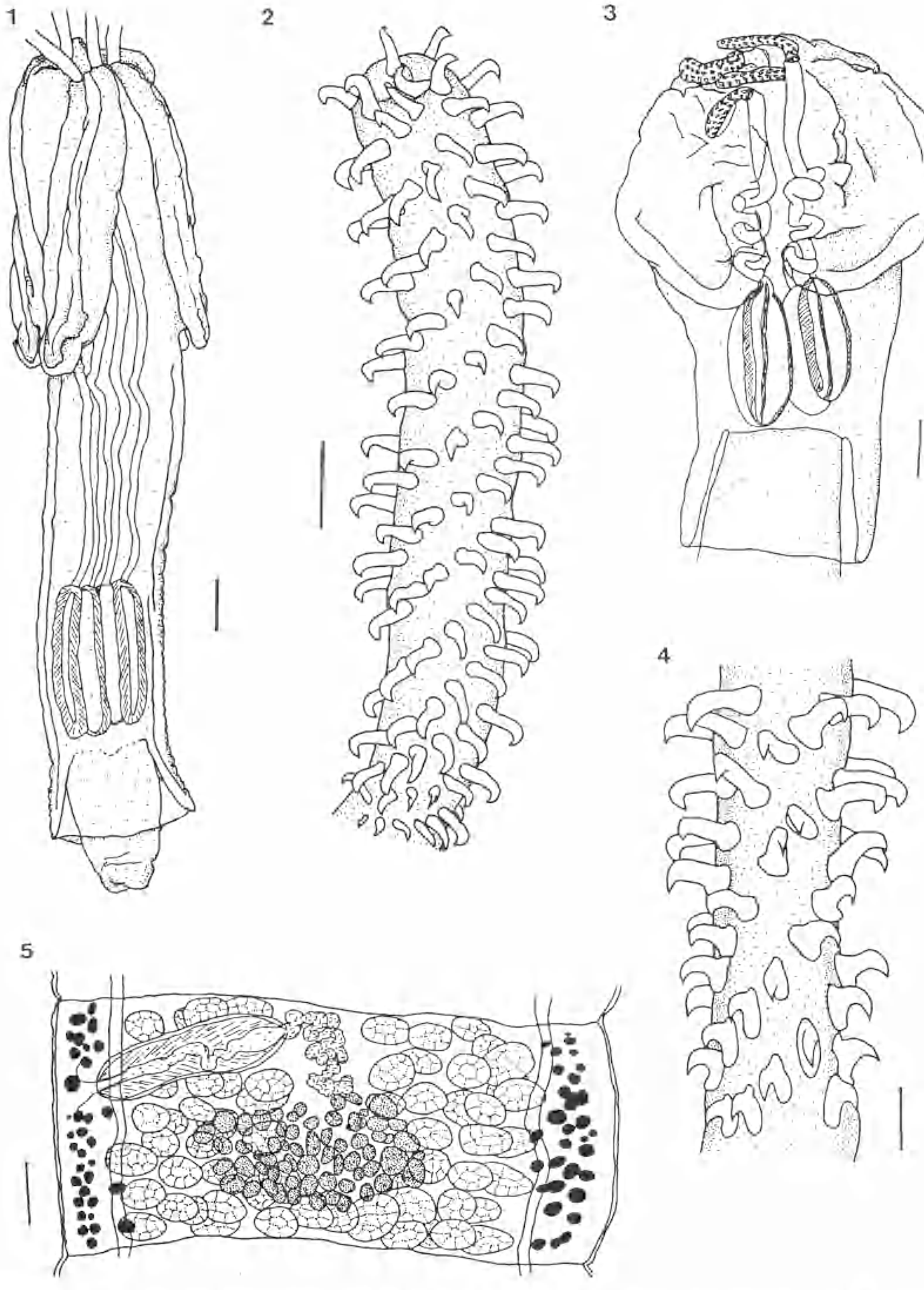
***Nybelinia africana*** Dollfus, 1960 (Figs 3–5)

*Material examined*

From unidentified shark: 1 adult, Queensland, coll. J. C. Pearson (QM G 218169).

*Description*

SL = 1780 (Fig. 3); SW = 1134; pbo = 930; pv = 840; pb = 523; vel = 417; BL = 439 (423–459); BW = 163 (157–171); BR = 2.7:1; SP = 1.8:1.6:1. TW metabasal = 47–50. Basal tentacular swelling absent. Tentacle sheaths spirally coiled; TSW = 65–70. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen. Retractor muscles




FIGURES 1–2. *Nybelinia aequidentata* Shipley & Hornell, 1906 from *Dendrochirus zebrae*. QM G 218031. **1**. Scolex. **2**. Homeomorphous armature with falciform hooks. Scale bars: Figure 1, 500 µm; Figure 2, 100 µm. FIGURES 3–5. *Nybelinia africana* Dollfus, 1960 from an unidentified shark. QM G 218169. **3**. Scolex. **4**. Basal and metabasal armature. **5**. Mature proglottid. Scale bars: Figure 3, 200 µm; Figure 4, 20 µm; Figure 5, 100 µm.

originate in basal parts of bulbs. Tentacular armature consists of homeomorphous hooks along tentacle (Fig. 4). Tentacles not completely evaginated; metabasal armature differs distinctly from basal armature. Basal 2–3 rows of rosethorn-shaped hooks with distinct anterior extension of base, L = 14–16, 16–17; metabasal hooks larger, falciform with small base, strongly recurved at tip, L = 26–27; B = 10–13. Strobila 57 mm long, with about 215 acraspedote segments which enlarge in size towards end of strobila, maximum width 1.48 mm; velum straight or very slightly scalloped; first segments 15–30 x 600–675, mature segments (Fig. 5) wider than long, 220–470 x 650–970 (n = 4). Pre-gravid segments (with some eggs) 440–670 x 1150–1480 (n = 5); terminal pre-gravid segment with rounded end. In mature segments, genital pore ventro-submarginal, in anterior half or anterior third of segment; genital pore to anterior end 90–150 in mature and 180–200 in pre-gravid segments; genital pores alternate irregularly. Cirrus sac thin-walled, elongate, 370–480 x 70–100 (n = 5), length:width ratio 4.5:1 (3.7–5.0:1), distal pole directed anteromedially, nearly reaching anterior end of proglottid, cirrus unarmed; internal and external seminal vesicle absent. Vas deferens greatly coiled, extends to midline of segment, then posteriorly towards female genital complex. Testes of varying shape, 60–90 in diameter, arranged in single layer centrally and in double layer peripherally; testis number 50–71 per segment, between 5 and 8 testes anterior to cirrus (n = 5). Ovary follicular, in centre of segment, bilobed, each lobe 190–260 x 140–220, increasing in size along strobila. Vitelline follicles encircle medulla, follicles 30–50 in diameter. Ventral and dorsal osmoregulatory canals 30 in diameter, testes extend external to ventral canal but not beyond dorsal canal.

*Remarks*

The present specimen closely resembles *N. africana* Dollfus, 1960 as described by Dollfus (1960) and Palm (1999) in having rosethorn-shaped basal hooks, changing to falciform metabasal hooks of similar size and shape. Additionally, the segment morphology with number and size of segments, size of cirrus sac, testes and vitelline follicles, as well as arrangement of the genital complex is similar. However, some differences were observed between the present specimen and *N. africana*. The specimen from Australia differs in having 2 to 3 rows of basal hooks with a distinct anterior extension of the base (Fig. 4), which has not been reported in other specimens of *N. africana*. However, Dollfus (1960, figs 14, 17) illustrated comparable basal hooks, some with an anterior extension of the base. The scolex is larger in the Australian specimen (1780) compared with other material (1118–1568) (Palm et al. 1997) and the testis number is smaller. However, as most other morphological characters correspond, the specimen is identified as *N. africana* and the observed differences are considered to be due to intraspecific morphological variability. The present finding is a new locality record for the species.

***Nybelinia hemipristis*** sp. nov.
(Figs 6–9)

*Types*

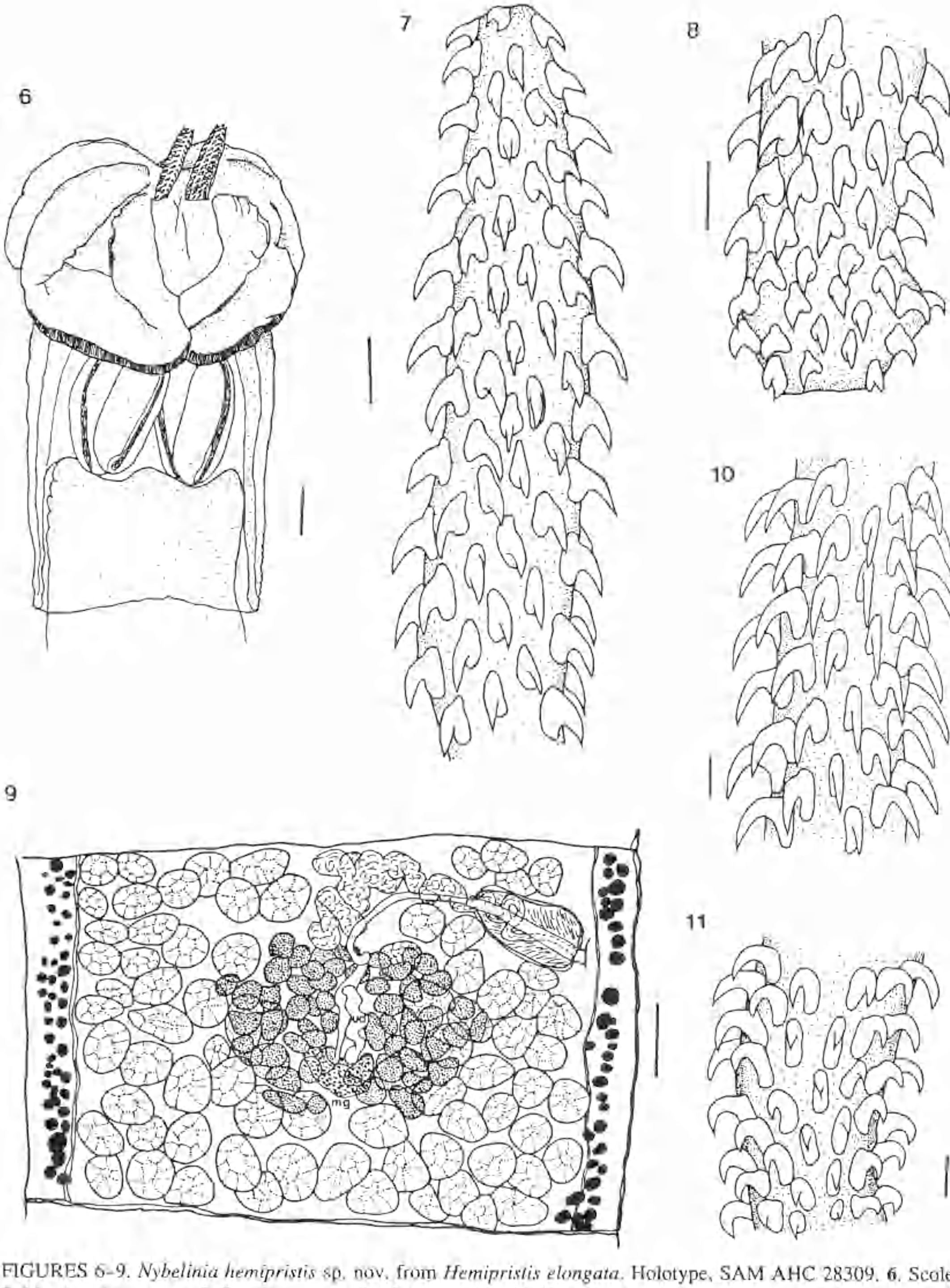
Holotype from stomach of *Hemipristis elongata* Klunzinger, 1871, Balgal, Queensland, coll. B. G. Robertson, 16.ix.1985 (SAM AHC 28309). Paratypes: 3 specimens, *Hemipristis elongatus*, Marchinbar Island, Northern Territory, coll. G. Cuthbertson, 25.v.1985 (SAM AHC 28310).

*Material examined*

Types.

*Description*

SL = 2030 (Fig. 6); SW = 1230; pbo = 1000; pv = 860; pb = 560; vel = 630; BL = 553 (550–560); BW = 218 (210–220); BR = 2.5:1; SP = 1.8:1.5:1. Tentacles short, massive, decreasing in diameter towards apical region; basal tentacular swelling absent. TW basal and metabasal = 75–85, TW apical = 37.5–62.5. Tentacle sheaths straight (TSW = 50–60), prebulbar organs and muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate in basal parts of bulbs. Tentacular armature homeoacanthous, homeomorphous (Fig. 7); distinctive basal armature absent (Fig. 8). Hooks slender, rosethorn-shaped with anterior elongation of base, increasing in size from basal (L = 15.5–30.0; B = 16.3–20.0) towards metabasal regions (L = 35.0–40.0; B = 25.0–27.5), then decreasing in size towards apical (L = 27.5–32.5; B = 15.0–20.0) region; hsr = 6. Strobila acraspedote, velum straight; 33 mm long, maximum width 1030, number of segments 300. Mature segments (Fig. 9) wider than long, 600–670 x 750–920. Genital pore submarginal, 200 from anterior end, alternating irregularly. Cirrus sac short and stout, 180–210 x 50–100 (n = 5), length:width ratio 2.9:1 (2.0–3.6:1), distal pole directed




FIGURES 6–9. *Nybelinia hemipristis* sp. nov. from *Hemipristis elongata*. Holotype, SAM AHC 28309. **6**. Scolex. **7**. Metabasal armature. **8**. Basal armature. **9**. Mature proglottid. Note short cirrus sac, the uterine duct (ud), and the Mehlis' gland (mg). Scale bars: Figure 6, 200 µm; Figures 7–8, 40 µm; Figure 9, 100 µm. FIGURES 10–11. *Nybelinia jayapaulazariahi* Reimer, 1980 from a 'sole'. QM G 207318. **10**. Metabasal armature. **11**. Basal armature. Scale bars: Figures 10–11, 10 µm.

anteromedially, not reaching anterior end of segments, cirrus unarmed; internal and external seminal vesicle absent. Vas deferens coiled, extends to midline of segment, then posteriorly towards female genital complex. Testes 84–97 in number, 55–85 in diameter centrally and 40–60 peripherally, distributed in single layer; arranged in 2 lateral groups, confluent posterior to ovary; extend between ovarian lobes, about 6–7 testes anterior to cirrus sac. Ovary in centre of segment, ovarian lobes 200–260 x 120–160. Vagina ventral to cirrus sac. Vitelline follicles encircle medulla; follicles 25–40 in diameter.

*Remarks*

The present specimens, with rosethorn-shaped hooks diminishing in size towards the apical armature and a strobila consisting of acraspedote segments, resemble *N. anthicosum* Heinz & Dailey, 1974. However, the species differ in having different scolex forms, tentacles, tentacular armatures and sizes. *N. anthicosum* has an elongated prominent velum, long tentacles and tentacular hooks which are distinctly spaced (see Heinz & Dailey 1974). The largest hooks occur in the 7th to 9th rows. *N. hemipristis* sp. nov. has a massive scolex with a shorter velum (Fig. 6), short tentacles and tentacular hooks which are tightly spaced along the tentacle. The largest hooks are in the 10th to 14th rows. In the last few hook rows, the size and number of hooks per half spiral row decrease rapidly (Fig. 7). In *N. anthicosum* the hook size diminishes gradually towards the apical part of the tentacle. As with *N. anthicosum*, *N. hemipristis* is a species without a characteristic basal armature and with a smaller basal than metabasal hook size, therefore belonging to species subgroup 'Aa' of Palm (1999).

The description of the strobilar characters of *N. hemipristis* demonstrates that this species has a very characteristic, short, stout cirrus sac, with a length:width ratio of 2 in some segments, a feature unusual in most species of *Nybelinia*. However, this character might prove to be of taxonomic significance in the future.

The new species is named after the elasmobranch host genus, *Hemipristis*.

***Nybelinia jayapaulazariahi*** Reimer, 1980
(Figs. 10–11)

*Material examined*

From 'sole', either *Synaptura nigra* Macleay, 1880 or *Aseraggodes macleayanus* (Ramsay, 1881): 1 postlarva, Moreton Bay, Queensland, coll. J. C. Pearson, 1968 (QM G 207318).

*Description*

SL = 1060; SW = 700; pbo = 470; pv = 450; pb = 365; BL = 323 (320–325); BW = 119 (85–135); BR = 2.7:1; SP = 1.3:1.2:1. TW = 32.5–35; hsr = 6. Basal tentacular swelling absent. Retractor muscles originate in basal parts of bulbs. Tentacular armature consists of homeomorphous slender uncinate hooks, L = 15.0–16.3, B = 11.2–13.7 (Fig. 10). Size of hooks diminishes towards basal part of tentacle, L = 11.2–13.7, B = 8.7–11.2 (Fig. 11).

*Remarks*

*N. jayapaulazariahi* was originally described from *Cynoglossus* sp. from the Bay of Bengal, India by Reimer (1980). Palm (1999) redescribed the species from another host, *Harpodon nehereus* (Hamilton-Buchanan, 1822), also from India. The tentacular armature has characteristic, slender, regularly curved hooks which increase in size towards the metabasal part of the tentacle. The present specimen, also from a 'sole', has a similar hook shape (compare Fig. 4 with Fig. 5 of Palm 1999) and bulb ratio, while it differs in having a larger scolex (1060 in the present specimen compared with 530 described previously) and hook size (11.2–16.3 in the current specimen compared with 5.6–11.2 in previous descriptions). However, the present specimen was in a poor state of preservation, and the larger scolex might be related to the slightly larger hook size. A small scolex of about 0.5–1.0 mm, together with the uncinate hook form, is characteristic for *N. jayapaulazariahi*, and soles seem to be important intermediate hosts. The present finding represents a new locality record for the species.

***Nybelinia mehlhorni*** sp. nov.
(Figs 12–14)

*Types*

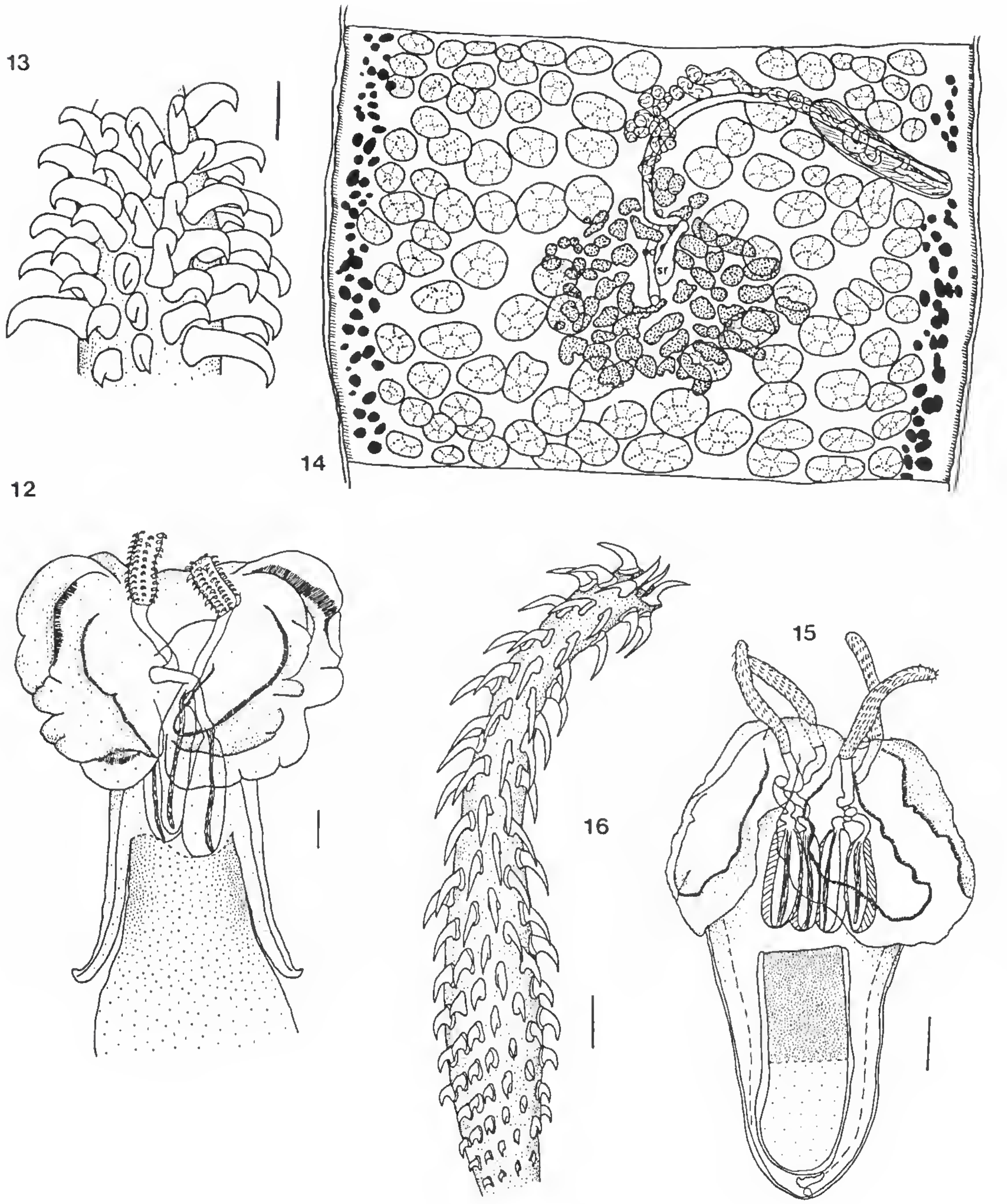
Holotype from stomach of *Hemigaleus microstoma* Bleeker, 1852, Heron Island, Queensland, coll. P. McBoarman, 20.xii.1995 (QM G 218032); paratype, same data (QM G 218033).

*Material examined*

Types.

*Description*

SL = 560 (Fig. 12); SW = 400; pbo = 330;




FIGURES 12–14. *Nybelinia mehlhorni* sp. nov. from *Hemigaleus microstoma*. Types, QM G 218032–3. **12**. Scolex. **13**. Metabasal and apical armature. **14**. Mature proglottid. Note the uterine duct (ud) and the seminal receptacle (sr). Scale bars: Figure 12, 50 µm; Figure 13, 10 µm; Figure 14, 50 µm. FIGURES 15–16. *Nybelinia scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) from *Diodon hystrix*. QM G 218035–7. **15**. Scolex. **16**. Basal and metabasal armature, external surface. Scale bars: Figure 15, 150 µm; Figure 16, 25 µm.

pv = 125; pb = 250; vel = 200; BL = 178 (150–200); BW = 58 (50–70); BR = 3.1:1; SP = 1.3:0.5:1. Tentacles short; basal tentacular swelling absent; TW = 22.5–27.5. Tentacle sheaths sinuous to spirally coiled (TSW = 17.5–20.0); muscular rings around basal part of tentacle sheaths seen. Retractor muscles originate in basal parts of bulbs. Tentacular armature homeoacanthous, homeomorphous (Fig. 13); distinctive basal armature absent. Hooks falciform, with stout base, elongated handle and strongly recurved tip. Hooks increase in size from basal (L = 3.5–7.5, B = 2.5–5.0) to metabasal region (L = 15.0–17.5, B = 6.3–8.7) then decrease towards apex (L = 11.3–13.8, B = 2.5–4.3); hsr = 7. Small worms, length 25 (16) mm, maximum width 950 (700) with 135 (90) segments. Strobila acraspedote, velum straight; pre-mature (testes visible) proglottids (Fig. 14) 80–280 long x 560–790 wide; mature segments (female genitalia developed) wider than long, 380–600 x 600–900; terminal segment 830 x 800. Genital pore almost lateral, 130–200 from anterior end (190 in terminal segment); pores alternate irregularly. Cirrus sac elongate, 170–220 x 40–60 (n = 5) in mature segments, length:width ratio 4.1:1 (2.8–5.5:1), distal pole directed anteromedially, not reaching anterior end of segments; cirrus unarmed, internal and external seminal vesicles absent. Vas deferens greatly coiled in midline of segments, extending posteriorly towards female genital complex. Testes 103–120 in number, 80 x 95 in size, smaller testes peripheral, 35–40 in size, distributed in single layer; testes in 2 lateral groups confluent posterior to ovary; 10–16 testes anterior to cirrus sac. Vagina tubiform, 30 in diameter, ventral to cirrus sac, passes anteromedially to midline, then posteriorly to ovary; seminal receptacle present, 60–90 x 25–50. Ovary in centre of segment, ovarian lobes 250–300 x 160–210. Vitelline follicles encircle medulla, follicles 30–45 in diameter. Uterine pore absent.

*Remarks*

Following Palm (1999), *N. mehlhorni* sp. nov. belongs to *Nybelinia* species without a characteristic basal armature and a basal hook size smaller than the metabasal one, thus belonging to the subgroup 'Aa'.

On the basis of the hook shape, the species resembles *N. aequidentata* (Shipley & Hornell, 1906) and *N. goreensis* Dollfus, 1960. While the former is much larger than the present specimen, the latter species has different scolex proportions as well as a different hook arrangement, as illustrated recently by Palm and Walter (2000).

*N. mehlhorni* sp. nov. also resembles *N. bengalensis* Reimer, 1980 in its falciform hooks and in hook size (Reimer 1980). However, *N. bengalensis* can be distinguished by having a distinctly different scolex form and size, a bulb ratio of about 2, long and slender tentacle sheaths and tentacles with spaced falciform hooks (Reimer 1980). By contrast, *N. mehlhorni* sp. nov. has short tentacles with hooks tightly spaced along the tentacle. The scolex (0.56 mm in total length) is much smaller.

The new species is named in honour of Prof. Heinz Mehlhorn, Heinrich-Heine-University, Düsseldorf.

## *Nybelinia schmidti* Palm, 1999

*Material examined*

From *Isurus oxyrhinchus* Rafinesque, 1810: 1 adult, Bicheno, Tasmania, coll. B. G. Robertson, 24.iv.1987 (SAM AHC 28313).

*Description*

SL = 1600; SW = 850; pbo = 1040; pv = 680; pb = 340; vel = 600; BL = 298 (270–330); BW = 131 (110–150); BR = 2.3:1; SP = 3.0:2.0:1. TW basal = 45–48, TW metabasal = 30.0–32.5; hsr = 5–6. Basal tentacular swelling absent. Tentacle sheaths spirally coiled, TSW = 25–40. Prebulbar organs absent, muscular rings present around the tentacle sheaths. Retractor muscles originate in basal part of bulbs. Tentacular armature homeoacanthous, homeomorphous, consisting of massive rosethorn-shaped hooks with anterior extension of base, size in metabasal region L = 13.8–15.0, B = 11.3–12.5, decreasing towards base, L = 8.8–11.3, B = 6.2–8.8. Characteristic basal armature absent. Strobila immature with few segments, acraspedote; segments wider than long (660–690 x 15–60).

*Remarks*

The present specimen closely resembles that of the type, also from *Isurus oxyrhinchus* (syn. *Isurus glaucus*), in having similar scolex proportions and almost identical hook sizes. Other species with a similar tentacular armature are *Nybelinia strongyla* Dollfus, 1960 and *Heteronybelinia australis* sp. nov. (*vide infra*). While the latter species differs in having homeomorphous hooks of different sizes on the internal and external tentacle surfaces as well as smaller basal hooks, *N. strongyla* differs in scolex proportions and larger hook sizes. The present record extends the range of distribution from the South African to the southern Australian coast.

***Nybelinia scoliodoni*** (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996)
(Figs 15–16)

*Material examined*

From *Diodon hystrix* Linnaeus, 1758: Heron Island, Queensland, 2 postlarvae, coll. J. Sakanari, 23.viii.1986 (QM G 218034); 8 postlarvae, coll. M. K. Jones, 6.vii.1995 (QM G 218035–218037); 8 postlarvae, coll. T. H. Cribb, Jan. 1997 (QM G 218038–218041).

From *Makaira indica* (Cuvier, 1832): 1 postlarva, Cape Bowling Green, Queensland, coll. P. Speare, 18.ix.1987 (SAM AHC 21351).

From *Istiophorus platypterus* (Shaw & Nodder, 1792): Whitsunday Island, Queensland, coll. P. Speare, 5.xii.1988 (SAM AHC 21351).

From *Carcharhinus limbatus* (Valenciennes, 1839): 1 adult, stomach, Bremer Island, Northern Territory, coll. J. Stevens, 29.v.1985 (SAM AHC 28314).

*Description*

SL = 1350, 1115 (Fig. 15); SW = 860, 800; pbo = 670, 520; pv = 230, 210; pb = 300, 320; vel = 330, 330; app = 310, 200; BL = 288 (280–300), 282 (260–300); BW = 115 (110–120), 125 (120–130); BR = 2.5:1, 2.3:1; SP = 2.2:0.8:1, 1.6:0.7:1. Tentacles nearly completely evaginated, TL = 390, 375; basal tentacular swelling absent. TW at basal armature 35, 30; TW at metabasal armature 50, 45; TW at apex 30, 25. Tentacle sheaths sinuous, TSW = 30, 40; prebulbar organs and muscular rings around basal part of tentacle sheaths not visible. Retractor muscles originate in basal parts of bulbs. Metabasal armature homeoacanthous, homeomorphous; distinctive basal armature present (Fig. 16). Basal armature consists of about 10 rows with compact rosethorn-shaped hooks, increasing in size from L = 4.5, B = 3.9 (row 1) to L = 19.5, B = 11.7 (row 10). From row 11, hook form changes to slender spiniform, L = 22.7, B = 13.0. Metabasal and apical hooks L = 29.9, with small base, B = 11. Number of hooks per half row (hsr) 6–7 in basal region, decreasing to 5 in metabasal and apical regions.

*Remarks*

*Nybelinia scoliodoni* is a widely distributed tentaculariid and is here recorded for the first time from Australian waters. The species is easily recognised by its rosethorn-shaped basal armature of about 11 rows which is followed by long, spiniform metabasal hooks. The present specimens correspond with the description given by Palm (1999) in having a similar armature and bulb ratio. They differ in having a larger scolex and hook size. However, they correspond closely to the original description of *Nybelinia* (= *Tentacularia*) *scoliodoni* of Vijayalakshmi et al. (1996). The present findings constitute three new host records. *C. limbatus* has been recorded previously as a definitive host for *N. scoliodoni* by Palm (1999). The specimens described here are the same as those reported by Speare (1999).

***Nybelinia strongyla*** Dollfus, 1960
(Figs 17–20)

*Material examined*

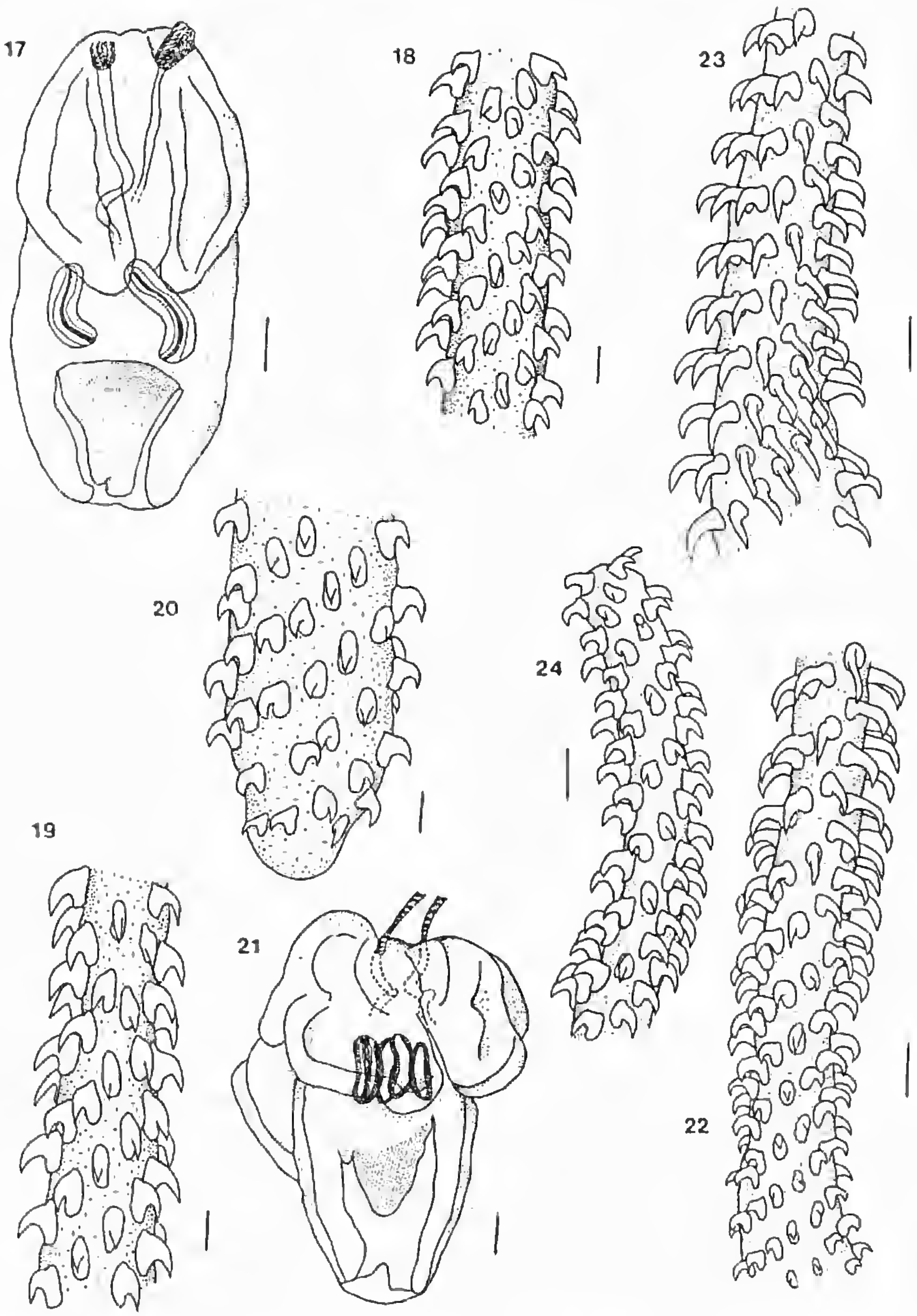
From *Argyrosomus hololepidotus* Lacépède, 1802: 2 postlarvae from stomach, Murray Mouth, South Australia, coll. M. G. O'Callaghan, May 1992 (SAM AHC 28345).

From *Johnius vogleri* (Bleeker, 1853): 1 postlarva from body cavity, Heron Island, Queensland, coll. J. Reddich, Jan 1997 (QM G 218109).

*Description*

Postlarvae from *A. hololepidotus*: SL = 1303, 1566 (Fig. 17); SW = 648, 796; pbo = 700, 781; pv = 647, 764; pb = 292, 355; vel = 332, 326; app = 374, 429; BL = 286 (244–292), 355 (334–380); BW = 86 (82–90), 98 (92–107); BR = 3.3:1, 3.6:1; SP = 2.4:2.2:1, 2.2:2.2:1. Tentacles not completely evaginated; basal tentacle swelling absent. TW = 50–58, 43–45. Tentacle sheaths sinuous, TSW = 36–40, 36–40; prebulbar organs and muscular rings around basal part of tentacle sheaths not visible. Retractor muscles originate in basal part of bulbs. Tentacle armature homeoacanthous, homeomorphous (Fig. 18); distinctive basal armature absent. Hooks slender, rosethorn-shaped, increasing in size from basal towards metabasal part of tentacle. Metabasal hooks L = 17.5–20.0; B = 13.8–16.3; basal hooks L = 10.0–12.5; B = 10.0–12.5; hsr = 7.

Postlarva from *J. vogleri*: SL = 1880; SW = 1660; pv = 680; pb = 440; BL = 308 (300–325); BW = 129 (115–150); BR = 2.4:1;




FIGURES 17–18. *Nybelinia strongyla* Dollfus, 1960 from *Argyrosomus hololepidotus*. SAM AHC 28345. **17**. Scolex. **18**. Metabasal armature. Scale bars: Figure 17, 150 µm; Figure 18: 15 µm. FIGURES 19–20. *Nybelinia strongyla* from *Johniops vogleri*. QM G218109. **19**. Metabasal armature. **20**. Basal armature. Scale bars: Figure 19–20: 10 µm. FIGURES 21–24. *Nybelinia thyrsites* Korotaeva, 1971 from *Trachurus declivis*. QM G 214194–5. **21**. Scolex. **22**. Basal armature. **23**. Metabasal armature with falciform hooks. **24**. Apical armature with rosethorn-shaped hooks. Scale bars: Figure 21, 200 µm; Figures 22–24, 25 µm.

SP = –:1.5:1. TW basal = 37–40, TW metabasal = 30–33. Basal tentacular swelling absent. Tentacle sheaths straight; TSW = 20–25. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths absent. Retractor muscles originate in basal part of bulbs. Armature homeoacanthous, homeomorphous (Fig. 19); characteristic basal armature absent (Fig 20). Hooks rosethorn-shaped with anterior extension of basal plate; hooks in basal part of tentacle smaller (L = 7.5–10.0; B = 7.5–9.5) than in metabasal (L = 13.8–16.3; B = 10.0–12.5) armature. Number of hooks per half spiral (hsr) diminishes from 6–7 in metabasal region to 5–6 in apical part of tentacle.

*Remarks*

*Nybelinia strongyla* Dollfus, 1960 was described from a postlarva from the west coast of Africa, and is characterised by the homeoacanthous tentacular armature with slender rosethorn-shaped hooks, reaching a size of up to 16 in the metabasal armature. Palm and Walter (2000) described adult specimens of *N. strongyla* from Africa. The present specimens correspond closely in their tentacular armature as well as in scolex proportions to those specimens described by Dollfus (1960) and Palm and Walter (2000). Minor variations in the hook pattern are observed within *N. strongyla* but are difficult to define, and many scolex characters within tentaculariids appear to be variable (Palm 1999, Palm and Walter 2000). Therefore, the postlarvae described above are identified as *N. strongyla*. However, some doubt surrounding the identification remains. Further studies are needed to determine whether postlarvae with rosethorn-shaped hooks as described above are conspecific with the African material, or whether they belong to a new species of *Nybelinia*. *Argyrosomus hololepidotus* is a new host record, and the distribution of the species is extended to the southern Australian coast.

The specimen from *J. vogleri*, with rosethorn-shaped hooks, resembles *N. lingualis*, *N. schmidti*, *N. sphyrnae*, *N. strongyla* and *N. thyrsites*. It differs from *N. lingualis* in having basal hooks with an anterior extension of the basal plate, and from *N. thyrsites* in having differently shaped metabasal hooks and a larger bulb ratio (see below). *N. schmidti* differs in having smaller hooks and different scolex proportions. *N. sphyrnae* differs in having slender, more uncinate hooks in the metabasal armature, while the hooks are more massive rosethorn-shaped in *N. strongyla*. In the present specimen, the basal hook length is slightly smaller than described by Palm and Walter (2000) for *N. strongyla*. However, the metabasal hooks are the same size. Although the scolex proportions were difficult to measure in the present specimen, it is also identified as *N. strongyla*, representing a new host and locality record.

### *Nybelinia thyrsites* Korotaeva, 1971
(Figs 21–24)

*Material examined*

From *Trachurus declivis* Jenyns, 1841: 2 postlarvae from stomach wall, Crayfish Bay, Tasmania, coll. K. B. Sewell, 11.v.1987 (QM G 214194, 212145).

From *Carcharhinus brachyurus* (Günther, 1870): 1 adult from stomach, Goolwa, South Australia, coll. R. Martin, 28.x.1985 (SAM AHC 28312).

From *Mustelus antarcticus* Günther, 1870: 1 adult from stomach, Goolwa, South Australia, coll. R. Martin, 28.x.1985 (SAM AHC 28311).

*Description*

SL = 2032, 1550 (Fig. 21); SW = 1520, 700; pbo = 1024, 610; pv = 640, 500; pb = 368, 520; vel = 992, 490; app = 496; BL = 358 (355–365), 495 (490–500); BW = 117 (114–120), 155 (140–170); BR = 3.1:1, 3.2:1; SP = 2.8:1.7:1, 1.2:1:1. Tentacle sheaths spirally coiled; TSW = 51–57, 35–45. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths present. Retractor muscles originate in basal part of bulbs. Tentacles long (TL = 832) and slender, basal tentacular swelling absent; TW basal = 38–44, 25–30; TW metabasal = 57.0, 57.7–62.5; TW apical 32.0, 27.5. Characteristic basal armature present (Fig. 22), consisting of about 7–8 rows of homeomorphous, rosethorn-shaped hooks with slight anterior extension, increasing in size towards metabasal armature (1st row hooks: L = 9.5–11.0, B = 8.0–11.0, L = 7.5–8.7, B = 6.3–7.5; 8th row: L = 15.8–17.4, L = 16.2–17.5, B = 11.0–12.6, B = 10.0–12.5). Metabasal armature of about 12–14 rows of hooks, with largest hooks in rows 12–17. Metabasal armature with slender falcate to falciform hooks (L = 21.7–26.9, B = 8.7–11.0; L = 21.3–24.0, B = 11.3–12.5) (Fig. 23). Apical hooks rosethorn-shaped, with hook form changing from slender rosethorn-shaped with slight anterior extension to rosethorn-shaped with distinct anterior extension (Fig. 24).

Hooks diminish in size towards apical region (34th row of hooks: L = 14.2–15.8, B = 11.0–14.2); hsr basal: 6–7; hsr metabasal and apical: 6.

*Remarks*

*N. thyrsites* was redescribed in detail by Beveridge and Campbell (1996). The present material corresponds with the redescription given. In addition, the basal hook form differs from the metabasal and apical hooks; thus, the species belongs to subgroup 'Ba' of Palm (1999). The present specimens from *Trachurus declivis* provide a further example in which the postlarvae can be larger than adult worms, and also show variable scolex measurements depending on the state of contraction. *Trachurus declivis* and *Carcharhinus brachyurus* are new hosts for *N. thyrsites*.

***Nybelinia victoriae*** sp. nov.
(Figs 25–26)

*Types*

Holotype from body cavity of *Lepidotrigla modesta* Waite, 1899, Port Phillip Bay, Victoria, coll. R. Norman, 17.iii.1989 (SAM AHC 28343); paratype, same data (SAM AHC 28344).

*Material examined*

Types.

*Description*

SL = 1030, 1050 (Fig 25); SW = 700, 650; Pbo = 570, 450; Pv = 350, 320; Pb = 315, 320; BL = 310 (300–315), 310 (305–320); BW = 124 (115–135), 116 (110–125); BR = 2.5:1, 2.7:1; SP = 1.8:1.1:1, 1.4:1.0:1. Tentacles elongate; basal tentacular swelling absent. TW = 40.0–50.0, 45.0–50.0. Tentacle sheaths sinuous to spirally coiled (TSW = 40.0–50.0, 35.0–40.0); prebulbar organs and muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate in basal part of bulbs. Armature homeoacanthous, homeomorphous (Fig. 26); distinctive basal armature absent. Hooks falciform, with stout base, elongated handle and strongly recurved tip. Hooks increase in size from basal (L = 7.5–10.0, B = 6.3–8.8) to metabasal region (L = 12.5–15.0, B = 7.0–8.0) and decrease towards apical (L = 11.3–12.5, B = 6.3–8.0) part of tentacle; hsr = 7.

*Remarks*

This species, with a tentacular armature consisting of slender falciform hooks, increasing in size towards the metabasal region and decreasing in size towards the apical region, resembles *Nybelinia aequidentata* Shipley & Hornell, 1906; *N. syngenes* Pintner, 1927; *N. anantaramanorum* Reimer, 1980; and *N. bengalensis* Reimer, 1980. While the former two species differ in having different scolex proportions and distinctly larger hooks (see remarks on *N. aequidentata*), the present specimens are most similar to *N. bengalensis* and *N. anantaramanorum*. *N. anantaramanorum* has larger hooks and was considered a *species inquirenda* by Palm and Walter (2000). *N. bengalensis* differs in having different scolex proportions, including very short bulbs (BR < 2) (Reimer 1980). Thus, the present specimens represent a new species here named *Nybelinia victoriae* sp. nov., the specific epithet being derived from the Australian state from which samples were collected. With hook size smaller in the basal rather than the metabasal region, the species is considered to belong to subgroup 'Aa' of Palm (1999).

Genus ***Heteronybelinia*** Palm, 1999

***Heteronybelinia australis*** sp. nov.
(Figs 27–30)

*Types*

Holotype from stomach of *Carcharhinus amboinensis* (Muller & Henle, 1839), St Lawrence, Queensland, coll. B. G. Robertson, 29.x.1985 (SAM AHC 28315); paratype, same data (SAM AHC 28316).

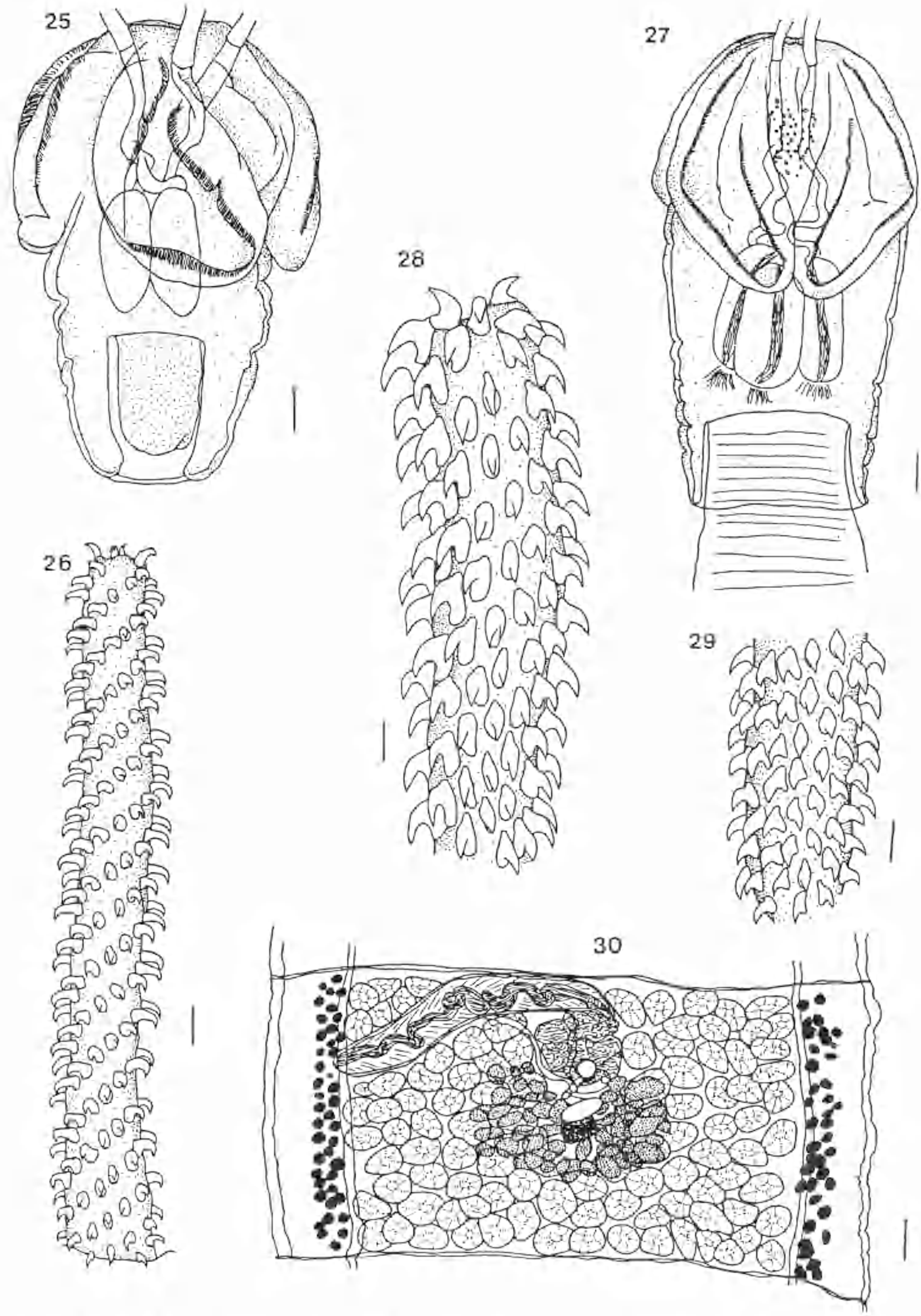
*Material examined*

From *Carcharhinus amboinensis*: types.

From *Carcharhinus brachyurus*: 1 specimen, Goolwa, South Australia, coll. R. Martin, 28.x.1985 (SAM AHC 28317).

*Description*

SL = 1190, 1210 (Fig. 27); SW = 660, 680; pbo = 650, 700; pv = 530, 650; pb = 350, 310; vel = 220, 190; BL = 313 (305–320), 308 (290–340); BW = 138 (125–150), 119 (110–130); BR = 2.3:1, 2.6:1; SP = 1.9:1.7:1, 2.3:2.1:1. Tentacle sheaths spirally coiled. TSW = 27.5–32.5, 25.0–35.0. Tentacles robust, TL = 255–290, increasing in width towards apex. TW basal and metabasal 30.0–32.5; basal tentacular swelling absent. Prebulbar organs absent; muscular rings




FIGURES 25–26. *Nybelinia victoriae* sp. nov. from *Lepidotrigla modesta*. Types, SAM AHC 28343–4. **25**. Scolex. **26**. Basal and metabasal armature. Scale bars: Figure 25, 100 μm; Figure 26, 20 μm. FIGURES 27–30. *Heteronybelinia australis* sp. nov. from *Carcharhinus amboinensis*. Types, SAM AHC 28315–6. **27**. Scolex. **28**. Metabasal armature. **29**. Basal armature. **30**. Mature proglottid. Note the uterine pore. Scale bars: Figure 27, 100 μm; Figures 28–29, 10 μm; Figure 30, 50 μm.

around basal parts of tentacle sheaths present. Retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous, with hooks tightly spaced along tentacle (Fig. 28); characteristic basal armature absent (Fig. 29). Hooks massive, rose-thorn shaped, with slight anterior extension of base, increase in size from basal towards metabasal armature. Hook size differs on bothridial/antibothridial (L = 12.5–15.0, B = 11.3–13.7) and antibothridial/bothridial (L = 11.3–12.5, B = 7.0–8.7) tentacle surfaces (Fig. 28), with two tentacles having largest hooks on bothridial surfaces and two other tentacles having largest hooks on antibothridial surfaces. Basal hooks L = 5.0–7.5, 7.5–8.7; B = 8.7–10.0 (internal) and L = 5.0–6.3, 5.0–7.5; B = 3.8–5.0, 5.0–6.3 (external); hsr = 6–7. Strobila only very slightly craspedote, velum scalloped; total length 18.0 and 15.0 mm, maximum width 640 and 730, with 125 and 155 segments. In holotype, terminal segment pre-mature (320 x 550), segments wider than long, 231 x 630. Genital pores ventro-submarginal, 60 from anterior margin; alternate irregularly. Cirrus sac of pre-mature segments elongate and slender, 210–230 x 35–50 (n = 5), length:width ratio 5.3:1 (4.6–6.0:1), with distal pole directed anteromedially, reaching anterior end of segment (Fig. 30); cirrus unarmed; internal and external seminal vesicles absent. Vas deferens coiled, extends posteriorly from cirrus sac towards female genital complex. Testes 106–130 in number, smallest testes at margin of medulla, distributed in 1–2 layers; in 2 lateral groups, confluent posterior to ovary; extend between ovarian lobes; 8–10 testes anterior to cirrus sac. Ventral osmoregulatory canal 15 in diameter, internal to sinuous dorsal canal, 5 in diameter; 24 prominent bands of longitudinal muscles on each side of strobila. Segments in paratype mature, wider than long (240 x 700 to 380 x 720). Genital pores 110 from anterior margin. Cirrus sac of mature segments (Fig. 30) elongate and slender, 260–320 x 50–60 (n = 5), length:width ratio 5.2:1 (4.3–5.8:1). Central testes 45–65 in diameter, smallest testes peripheral, 30–50 in diameter, distributed in 1–2 layers; ovarian lobes 110–200 x 80–110, seminal receptacle 50–65 x 25–30.

*Remarks*

*Heteronybelinia australis* sp. nov. has a unique armature. The tentacular hooks are tightly spaced and appear homeomorphous along the tentacle. However, the hook sizes differ on the bothridial and antibothridial tentacular surfaces. In addition, two tentacles have the largest hooks on the bothridial surfaces while the other two tentacles have the largest hooks on the antibothridial surfaces. Whether this armature pattern is unique or whether it occurs in other tentaculariid species remains to be determined.

The specific epithet indicates the occurrence of the species in Australian waters.

***Heteronybelinia estigmena*** (Dollfus, 1960)
(Figs 31–36)

*Material examined*

From *Carcharhinus limbatus* Valenciennes, 1839: 16 adults from spiral valve, Geraldton, Western Australia, coll. B. G. Robertson, 27.xi.1986 (SAM AHC 21352, 28318); 4 adults from spiral valve, Nickol Bay, Western Australia, coll. B. G. Robertson, 11.xi.1986 (SAM AHC 28319); 3 adults from spiral valve, Darwin Harbour, Northern Territory, coll. B. G. Robertson, 28.viii.1986 (SAM AHC 28320); 6 adults from spiral valve, Fog Bay, Northern Territory, coll. B. G. Robertson, 4.x.1986 (SAM AHC 28329).

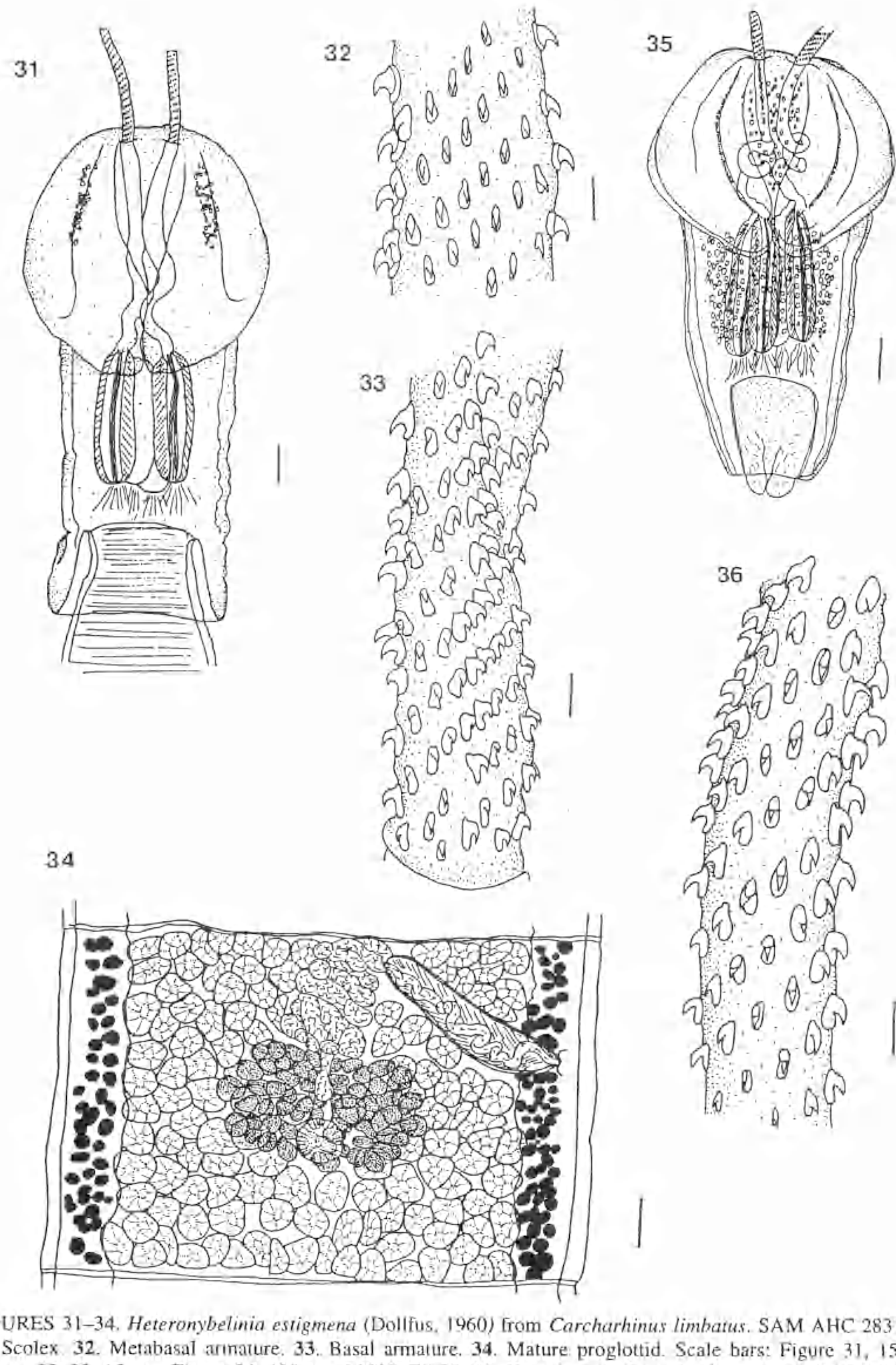
From *Carcharhinus amblyrhynchoides* (Whitley, 1934): 2 adults from spiral valve, Tommy Cut Mouth, Northern Territory, coll. B. G. Robertson, 10.ix.1986 (SAM AHC 28321).

From *Carcharhinus* sp: 3 adults from spiral valve, Queensland, coll. B. G. Robertson, Oct. 1985 (SAM AHC 18322).

From *Sarda australis* (Macleay, 1881): 9 postlarvae from gill arches, Heron Island, Queensland, coll. M. K. Jones, Jan. 1991 (QM G 218042–218046).

*Description*

*Adult:* SL = 1650, 1500 (Fig. 31); SW = 790, 770; pbo = 820, 820; pv = 690, 610; pb = 480, 430; ppb = 110, 80; vel = 330, 320; BL = 455 (440–480), 425 (420–430); BW = 133 (130–140), 120 (118–122); BR = 3.4:1, 3.6:1; SP = 1.7:1.4:1, 1.9:1.4:1. Tentacles long, slender (TL = 520, 560), TSW = 42.5–47.5, 45.0–55.0; TW basal 45–50, 42.5–45; TW apical 25–30, 27.5–32.5; basal tentacular swelling absent. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths visible in one specimen. Retractor muscles originate at bases of bulbs. Tentacular armature homeoacanthous, heteromorphous, no characteristic basal armature present (Figs 32–33). Hooks rosethorn-shaped, increase in size towards metabasal part of




FIGURES 31–34. *Heteronybelinia estigmena* (Dollfus, 1960) from *Carcharhinus limbatus*. SAM AHC 28318–20. **31**. Scolex. **32**. Metabasal armature. **33**. Basal armature. **34**. Mature proglottid. Scale bars: Figure 31, 150 µm; Figures 32–33, 15 µm; Figure 34, 100 µm. FIGURES 35–36. *H. estigmena* from *Sarda australis*. QM G 218042–46. **35**. Scolex. **36**. Basal armature. Scale bars: Figure 35, 150 µm; Figure 36, 15 µm.

tentacle. Hook form varies from compact and rosethorn-shaped (bothridial) to smaller rosethorn-shaped hooks with elongated base (antibothridial). Hook size, metabasal, L = 11.3–12.5; B = 9.3–10.8 (bothridial) and L = 9.3–10.8; B = 10 (antibothridial), with largest hooks L = 13.8–15.0; B = 10.0–12.5 (bothridial); hooks diminish in size towards apical part of tentacle. Hook size in basal region L = 7.5–8.8; B = 6.3–10.0 (bothridial) and L = 5.0–7.5; B = 6.3–7.5 (antibothridial); hsr = 6–7. Strobila 56 mm long, maximum width 1250, about 280 acraspedote segments (Fig. 34). First segments behind velum short, enlarge in size, mature segments wider than long, from 500 x 840 to 700 x 1030. In mature segments, genital atrium ventro-submarginal, in anterior third of segment; genital pores alternate irregularly. Cirrus sac elongated, 300–450 x 80–110 (n = 5), length:width ratio 3.8–4.1:1, directed anteromedially, sac thin-walled; cirrus unarmed and coiled within sac. Ovary median, follicular, ovarian lobes 200–230 (length) x 110–170 (width), Mehlis' gland 80 in diameter, seminal receptacle 110 x 70; testes of variable shape, 60–80 x 30–60 (n = 5) in diameter, arranged in single layer; testes number 106–126 (n = 5) per segment, encircle female genital complex and occupy entire medulla except for region of female genital complex and anterior to it; 7–9 testes anterior to cirrus sac. Vitelline follicles 20–40 in diameter; egg diameter 20–25; ventral osmoregulatory canals along margins of cortex, 6 in diameter.

*Postlarva*: SL = 1650, 1500 (Fig. 35); SW = 790, 770; pbo = 820, 820; pv = 690, 610; pb = 480, 430; ppb = 110, 80; vel = 330, 320; BL = 460 (430–470), 445 (440–450); BW = 115 (110–120), 120 (118–122); BR = 4.0, 3.7; SP = 1.7:1.4:1, 1.9:1.4:1. Tentacles long, slender (TL = 550–580), TSW = 40–45; TW basal = 35–40, TW metabasal and apical = 30–40; basal tentacular swelling absent. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths present. Retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous; characteristic basal armature absent. Hook shape varies from compact, rosethorn-shaped (bothridial) to smaller rosethorn-shaped hooks with elongated base (antibothridial); hooks increase in size towards metabasal part of tentacle on bothridial and antibothridial surface (Fig. 36). Hook size, metabasal, L = 12.5–15.0, B = 11.8–13.3 (bothridial) and L = 11.3–12.5; B = 7.5–10.0 (antibothridial); basal L = 7.5–10.0; B = 8.8–11.3 (bothridial) and L = 5.0–7.5; B = 6.3–8.8 (antibothridial); hsr = 6–7.

*Remarks*

*Heteronybelinia estigmena* (Dollfus, 1960) is a well-described tentaculariid. Palm (1995) reported this cestode as *Nybelinia alloiotica* Dollfus, 1960 from *Carcharhinus limbatus* in the Atlantic, the same host species as in the present study. Palm (1999) and Palm and Walter (2000) provided additional information on the species. *H. estigmena* resembles *H. perideraeus* (Shipley & Hornell, 1906) and *H. elongata* (Shah & Bilqees, 1979) known from the coast of India. However, the hook size increases on both the bothridial and antibothridial tentacle surfaces in *H. estigmena*. In *H. elongata*, the hook size increases on the antibothridial tentacle surface only (Palm & Walter 1999), while in *H. perideraeus*, the basal and metabasal hook sizes are the same (Palm 1999). The present study represents the first record of the cestode from Australian waters. *Carcharhinus amblyrhynchoides* and *Sarda australis* represent new hosts for the species.

***Heteronybelinia pseudorobusta*** sp. nov.
(Figs 37–41)

*Types*

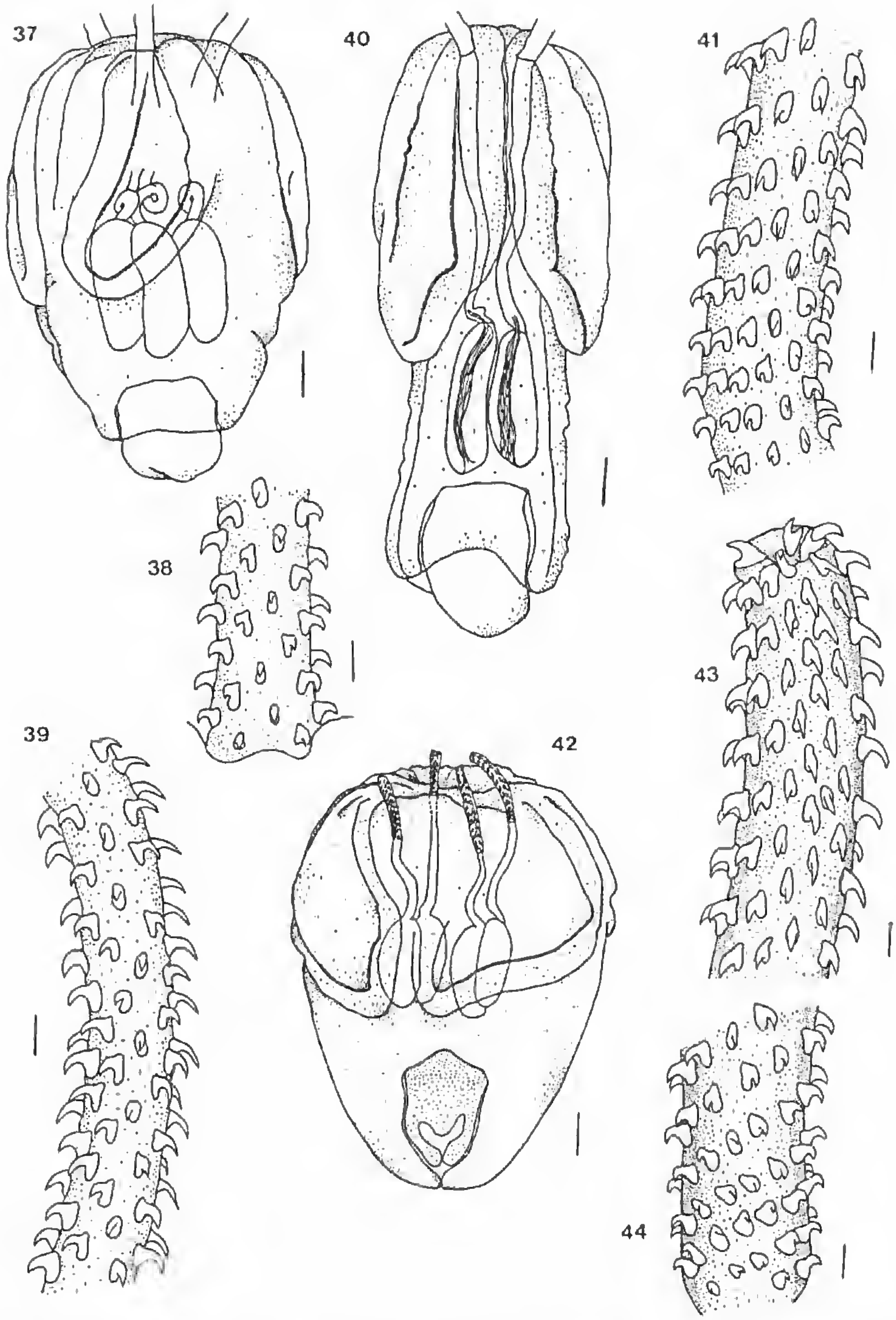
Holotype from gills of *Lepidotrigla modesta* Waite, 1899, Port Phillip Bay, Victoria, coll. R. Norman, 17.iii.1989 (SAM AHC 28341); 3 paratypes, same data (SAM AHC 28342).

*Material examined*

Types.

*Description*

*Small form* (holotype and one paratype): SL = 960 (Fig. 37), 730; SW = 660, 550; pbo = 570, 450; pv = 420, 270; pb = 285, 290; app = 220, 160; vel = 70, 60; BL = 280 (275–285), 298 (275–315); BW = 150 (145–155), 139 (110–165); BR = 1.9:1, 2.1:1; SP = 2.0:1.5:1, 1.6:0.9:1. Tentacle sheaths sinuous to spirally coiled; TSW = 45.0–47.5, 45.0–50.0; TW basal 45.0–50.0, metabasal 40.0–45.0, basal tentacular swelling absent. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen, retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous, characteristic basal armature absent (Fig. 38). Hook form changes from compact, rosethorn-shaped




FIGURES 37–41. *Heteronybelinia pseudorobusta* sp. nov. from *Lepidotrigla modesta*. **37**. Scolex of small form SAM AHC 28314. **38**. Basal armature. **39**. Metabasal armature. **40**. Scolex of large form SAM AHC 28342. **41**. Metabasal armature. Scale bars: Figure 37, 100 μm; Figures 38–39, 20 μm; Figure 40, 100 μm; Figure 41, 15 μm.
FIGURES 42–44. *Mixonybelinia cribbi* sp. nov. from *Platycephalus arenarius*. Holotype, QM G 218047. **42**. Scolex. **43**. Metabasal armature. **44**. Basal armature. Scale bars: Figure 42, 200 μm; Figures 43–44, 20 μm.

(bothridial) to more slender hooks with stout base (antibothridial) (Fig. 39). Hook size in metabasal armature ranged between L = 13.8–16.3; B = 11.3–13.8 (bothridial) and L = 16.3–17.5; B = 10.0–11.3 (antibothridial), hooks of basal part of tentacle smaller, between L = 10.0–11.0; B = 11.3–9.0 (bothridial) and L = 11.3–12.5; B = 8.8–10.0 (antibothridial), continuously increasing towards the tip; hsr = 6–7.

*Large form* (2 paratypes): SL = 1310 (Fig. 40); 1310; SW = 600, 620; pbo = 810, 780; pv = 580, 500; pb = 390, 380; app = 330, 330; vel = 280, 310; BL = 376 (360–390), 321 (310–330); BW = 124 (115–140), 121 (105–135); BR = 3.0:1; SP = 2.1:1.5:1. Tentacle sheaths sinuous to spirally coiled; TSW = 40–45, 42.5–47.5; TW basal 45.0–47.5, metabasal 30.0–35.0, 30.0–35.0. Basal tentacular swelling absent, prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous, characteristic basal armature absent. Hooks change from compact and rosethorn-shaped (bothridial) to more slender hooks with a stout base (antibothridial) (Fig. 41). Hook size in metabasal armature between L = 12.5–14.5; B = 11.3–12.5 (bothridial) and L = 14.5–15.5; B = 8.8–10.0 (antibothridial), hooks of basal part of tentacle small, between L = 8.8–10; B = 7.5–9.0 (bothridial) and L = 6.3–8.8; B = 6.3–7.5 (antibothridial), increasing in size towards tip; hsr = 6–7.

*Remarks*

*Heteronybelinia pseudorobusta* sp. nov. is characterised by a heteromorphous tentacular armature consisting of small basal hooks increasing in size towards the metabasal region. The hook shape varies from rosethorn-shaped to slender hooks with a stout base on different surfaces of the tentacle. Small basal hooks which gradually increase in size towards the metabasal armature are characteristic of *Heteronybelinia robusta* (Linton, 1890). However, in contrast to *H. pseudorobusta* sp. nov., *H. robusta* has minute basal hooks, less than 5 in length, and the hook form is uniform along the tentacle. In the present specimens, the basal hook size is larger and the hook form is rosethorn-shaped. All other *Heteronybelinia* species differ in having a different hook shape or arrangement. Thus, the present specimens belong to a new species, *H. pseudorobusta* sp. nov., the name being derived from the similarity in hook arrangement to *H. robusta* (Linton, 1890). *H. pseudorobusta* is a species without a characteristic basal armature and with basal hook sizes smaller than metabasal hook sizes. It therefore belongs to the *Heteronybelinia* species subgroup 'Aa' in Palm (1999).

*Heteronybelinia pseudorobusta* sp. nov. occurred in two different size groups, those smaller than 1 mm and those larger than 1.3 mm, respectively. Thus, the present description is an example of intraspecific morphological variability within species of *Heteronybelinia*, apparently due to scolex contraction during fixation.

## Genus *Mixonybelinia* Palm, 1999

### *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997)

*Material examined*

From *Macruronus novaezelandiae* (Hector, 1871): 1 postlarva, west coast of Tasmania, coll. K. Sewell, June 1986 (QM G 218067).

*Description*

SL = 3200; SW = 2750; pbo = 1750; pv = 850; pb = 1300; ppb = 80; vel = 950; app = 730; BL = 1226 (1150–1310); BW = 290 (240–320); BR = 4.2:1; SP = 1.3:0.7:1. Tentacle sheaths sinuous to spirally coiled; TSW = 100–130. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate in basal parts of bulbs. Basal tentacular swelling absent; TW basal = 110–120; TW metabasal = 115–135. Metabasal armature homeoacanthous, heteromorphous, characteristic homeomorphous basal armature consisting of about 6–7 rows of slender hooks with elongated shaft, stout base and strongly recurved at tip (L = 31.3–40.0, B = 18.8–27.5). Metabasal hooks strongly recurved, rosethorn-shaped with large base on antibothridial surface: L = 50.0–52.5, B = 37.5–42.5; slender falcate hooks with stout base on bothridial surface: L = 55.0–60.0, B = 27.5–30.0; hsr = 6.

*Remarks*

The present specimen is characterised by a homeomorphous basal armature of 6–7 rows of hooks and a heteromorphous metabasal armature of massive hooks, thus corresponding in form and size with specimens of *M. beveridgei* described from African waters by Palm et al. (1997). Other features are the large scolex size as well as TSW and TW. However, due to the contracted nature of the scolex of the current specimen, values for scolex and bulb proportions as well as the tentacle sheaths differed, indicating the variability of these characters due to the degree of contraction of the scolex. The present finding represents a new host and locality record for *M. beveridgei*.

### *Mixonybelinia cribbi* sp. nov.
(Figs 42–44)

*Types*

Holotype, postlarva from *Platycephalus arenarius* Ramsay & Ogilby, 1886, Heron Island, Queensland, coll. J. Reddick, Jan. 1997 (QM G 218047).

*Material examined*

Types.

*Description*

Scolex craspedote, SL = 2920 (Fig. 42); SW = 2200; pbo = 1700; pv = 1020; pb = 730; ppb = 220; vel = 760; app = 780; BL = 615 (600–630); BW = 232 (220–240); BR = 2.7:1; SP = 2.3:1.4:1. Tentacle sheaths short; TSW = 50–65. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate in basal part of bulbs. Basal tentacular swelling absent; TW basal = 70–75, TW metabasal = 65–75. Homeoacanthous, heteromorphous metabasal armature consisting of rosethorn-shaped hooks on bothridial and more slender hooks with stout base on antibothridial surface (Fig. 43); characteristic homeomorphous basal armature (Fig. 44) consisting of about 4 rows of slender hooks with enlarged base and strongly recurved at tip (L = 12.5–17.5, B = 10.0–15.0 to 8.8–11.3). Metabasal hooks strongly recurved, rosethorn-shaped with large base on antibothridial surface: L = 20.0–22.5, B = 18.8–21.3; slender falcate with stout base along bothridial surface: L = 21.3–23.7, B = 15.0–17.5; hsr = 6–7.

*Remarks*

*M. cribbi* sp. nov. resembles *M. beveridgei* in scolex size as well as in tentacular armature. Both species have a homeomorphous basal and a heteromorphous metabasal armature as well as a large scolex about 3 mm in length. However, *M. cribbi* sp. nov. is clearly distinguishable from *M. beveridgei* by having only 4 rows of basal hooks compared with 6 in *M. beveridgei*. In addition, the hooks have a distinctly enlarged base in *M. cribbi* and all hooks are smaller (20–24 in *M. cribbi* compared with 46–68 in *M. beveridgei*, see Palm et al. 1997). The new species was named after Dr T. H. Cribb, Department of Parasitology, University of Queensland, Australia.

### *Mixonybelinia edwinlintoni* (Dollfus, 1960)
(Figs 45–53)

*Material examined*

From *Sphyrna lewini* (Griffith & Smith, 1843): 10 adults from stomach, Flat Top Island, Queensland, coll. B. G. Robertson, 23.x.1985 (SAM AHC 28324); 1 adult, Geraldton, Western Australia, coll. B. G. Robertson, 27.xi.1986 (SAM AHC 28323).

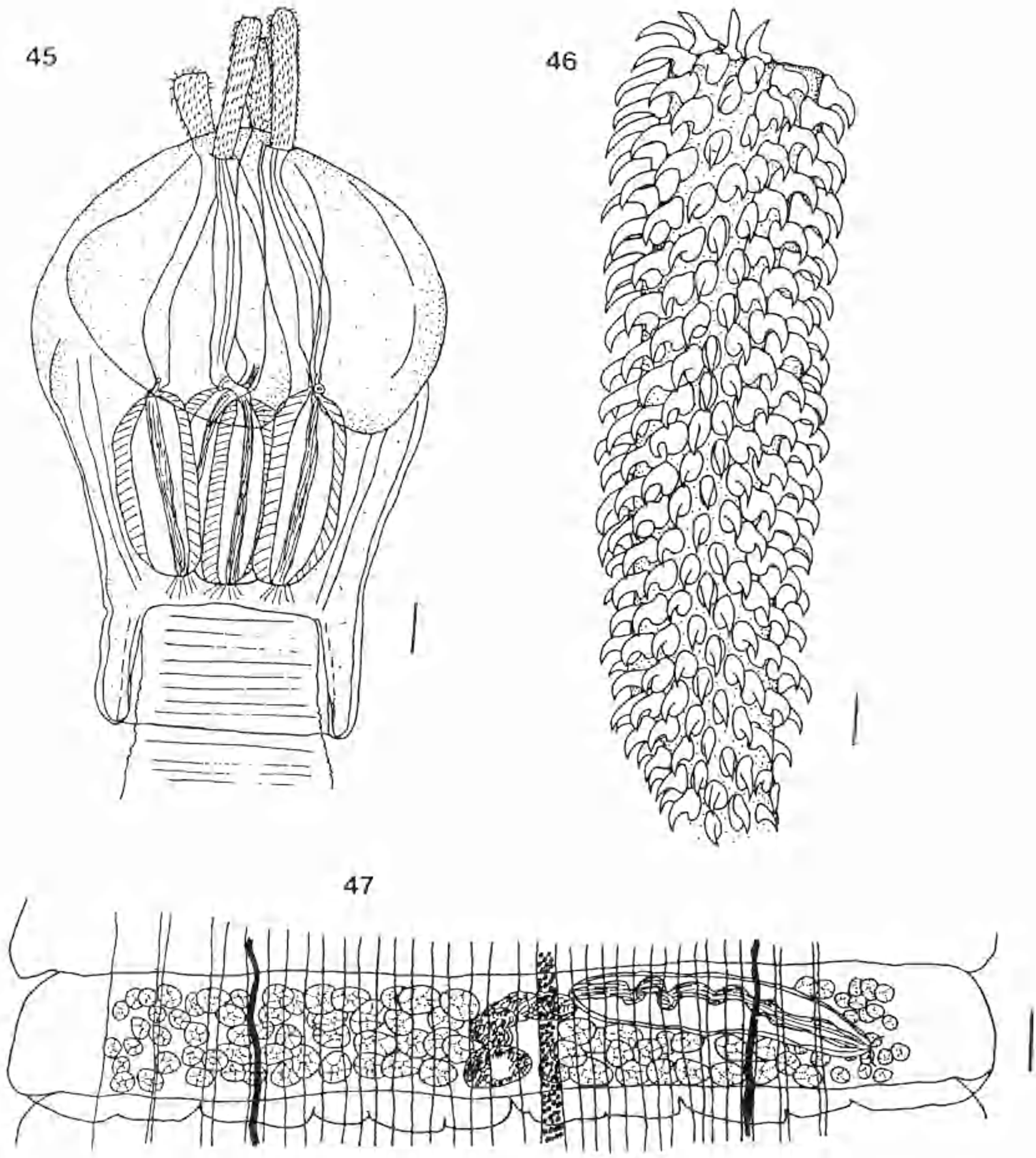
From *Rhynchobatus djiddensis* (Forsskål, 1775): 9 postlarvae from spiral valve, Moreton Bay, Queensland, coll. S. Butler, 17.iv.1980 (QM G 218048–218060).

From *Carcharhinus melanopterus* (Quoy & Gaimard, 1824): 1 postlarva, (QM G 4813).

*Description*

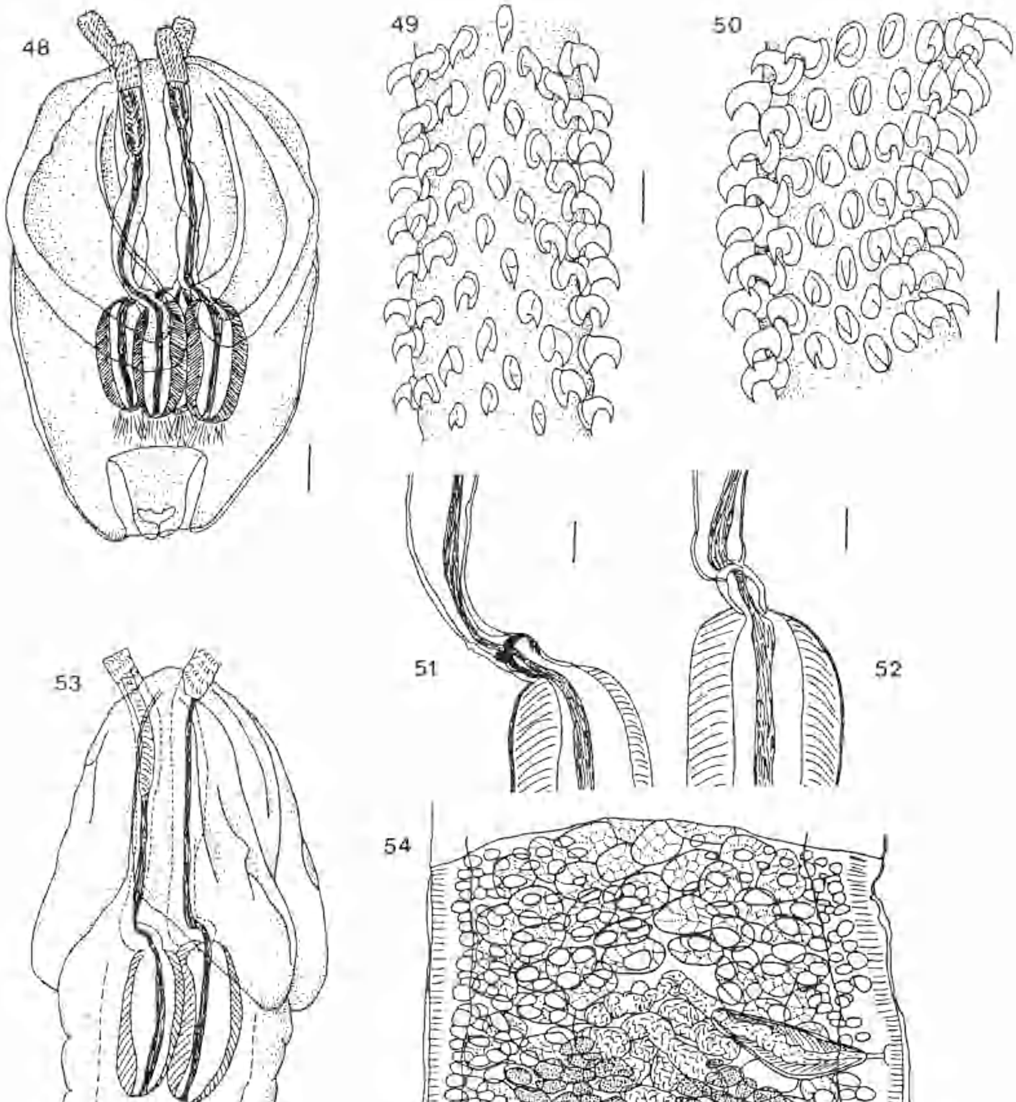
*Adults:* SL = 1780, 1620 (Fig. 45); SW = 1210, 1160; pbo = 1000, 1000; pv = 760, 690; pb = 620, 530; ppb = 60, 30; vel = 340, 330; BL = 585, 520, 520, 530, 490, within single specimen 580–600; BW = 235 (230–240); BR = 2.5:1; SP = 1.6:1.2:1. Tentacles robust; tentacle sheaths straight, TSW = 50–90. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths visible in some specimens. Retractor muscles originate in basal part of bulbs; basal tentacular swelling absent; TW basal = 60–65; TW metabasal = 70–75. Metabasal armature homeoacanthous, heteromorphous (Fig. 46); characteristic homeomorphous basal armature consisting of about 10 rows of slender falciform hooks (Fig. 46). Metabasal hooks strongly recurved along antibothridial surface: L = 20.0–25.0; B = 17.8–21.3; slender falcate hooks along bothridial surface: L = 32.5–35.0; B = 15.0–17.5. Basal hook size: L = 17.5–20.0, B = 10.0–13.8; hsr basal: 7–8; hsr metabasal: 8–9.

Largest cestode 53 mm, maximum width 880; 560 segments; strobila craspedote, velum irregularly scalloped, up to 50 wide; pre-mature (no ovary) segments (Fig. 47) wider than long, 100 x 1020 to 120 x 1020. Genital pores submarginal, in first third of segment; alternate irregularly. Cirrus sac elongate, 280–330 x 45–60 (n = 5) in mature segments, length:width ratio 5.7:1 (4.7–7.1:1), distal pole directed




FIGURES 45–47. *Mixonybelinia edwinlintoni* (Dollfus, 1960) from *Sphyrna lewini*. SAM AHC 28324. **45**. Scolex. **46**. Basal and metabasal armature. **47**. Pre-mature proglottid. Scale bars: Figure 45, 150 μm; Figure 46, 25 μm; Figure 47, 60 μm.

anteromedially, nearly reaching anterior end of segment; cirrus unarmed; internal and external seminal vesicles absent. Vas deferens coiled, extends to midline of segment, then posteriorly towards female genital complex. Testes in two groups, not confluent posterior to ovary, 80 (poral) and 116 (antiporal) (estimated), 30–40 in size (central), smallest testes at margin of medulla, external to osmoregulatory canal (15–25), distributed in 2–3 layers, extend anterior to cirrus sac; seminal receptacle present. Small vitelline follicles encircle medulla, between 24 longitudinal muscle bands. Osmoregulatory canals 5 and 20 in diameter.




FIGURES 48–52. *Mixonybelinia edwinlintoni* (Dollfus, 1960) from *Rhynchobatus djiddensis*. QM G 218048–60. **48**. Scolex. **49**. Basal armature. **50**. Metabasal armature, 20 rows from the base. **51–52**. Bulb with tentacle sheath. Scale bars: Figure 48, 150 µm; Figures 49–50, 25 µm; Figures 51–52, 50 µm. FIGURE 53. *M. edwinlintoni* from *Carcharhinus melanopterus*. QM G 4813. Scolex. Scale bar: 100 µm. FIGURE 54. *Kotorella pronosoma* (Stossich, 1901) from *Dasyatis fluviorum*. QM G 218063. Mature proglottid. Scale bar: 50 µm.

*Postlarvae* (from *R. djiddensis*): SL = 1600, 1500 (Fig. 48); SW = 1000, 1180; pbo = 1020, 950; pv = 680, 600; pb = 420, 470; ppb = 140, 120; vel = 280, 250; app = 280, 250; BL = 390 (370–410), 430 (410–440); BW = 188 (180–190), 163 (150–180); BR = 2.1:1, 2.6:1; SP = 2.4:1.6:1; 2.0:1.3:1. Tentacle sheaths straight, TSW = 40–85. Prebulbar organs absent, muscular rings and thickenings around basal part of tentacle sheaths visible in some specimens (Figs 51, 52). Retractor muscles originate in basal part of bulbs (Fig. 48); basal tentacular swelling absent; TW basal = 80, 80; TW metabasal = 70, 80. Homeomorphous basal armature of about 10 rows of slender falciform hooks (Fig. 49), metabasal armature homeoacanthous, heteromorphous (Fig. 50). Metabasal hooks strongly recurved along antibothridial surface: L = 22.5–25.0; B = 17.5–20.0; slender falcate hooks along bothridial surface: L = 23.8–26.3; B = 12.5–15.0. Basal hook size: L = 17.5–20.0, B = 12.5–13.8; hsr basal: 7–8; hsr metabasal: 8–9.

*Postlarva* (from *C. melanopterus*): SL = 1648 (Fig. 53); SW = 848; pbo = 912; pv = 768; pb = 432; ppb = 96; app = 320; vel = 240; BL = 429 (411–443); BW = 171 (158–177); BR = 2.5:1; SP = 2.1:1.8:1. Tentacles massive (TL = 630), TSW = 68–70; TW basal 77–80, TW metabasal 85–89, basal tentacular swelling absent. Prebulbar organs absent; muscular rings around basal part of tentacle sheaths not visible; retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous; characteristic basal armature absent. Hooks diminish in size towards base; hook shape varies from compact rosethorn-shaped (antibothridial) to slender rosethorn-shaped hooks with stout base (bothridial). Hook size, metabasal, rows 16–17, L = 23.7–25.2; B = 14.2–15.8 (antibothridial) and L = 25.2–26.8; B = 9.5–12.0 (bothridial); basal L = 17.4–19.0; B = 14.2–15.8 (antibothridial) and L = 17.4–19.0; B = 12.6–14.2 (bothridial); hsr = 7–8.

*Remarks*

Palm and Walter (2000) redescribed *Mixonybelinia edwinlintoni* (Dollfus, 1960) illustrating a distinctly different basal and metabasal armature within the species. While the metabasal armature has different hooks on the bothridial and antibothridial tentacle surface, the hooks of the basal armature appear to be homeomorphous. The arrangement of the hooks, together with their characteristic shape, and the scolex shape, indicate that the present specimens belong to *M edwinlintoni*. *Rhynchobatus djiddensis* and *Carcharhinus melanopterus* represent two new hosts for the species.

Prior to the re-description of *M. edwinlintoni*, Palm (1999) erected *Heteronybelinia heteromorphi*, a species which is also very similar to the present material. In *H. heteromorphi* the basal armature is heteromorphous, while in *M. edwinlintoni* it is homeomorphous. In addition, the type material of *H. heteromorphi* was described as being acraspedote while *M. edwinlintoni* is craspedote (Fig. 47). Interestingly, both species occur within the same host genus, *Sphyrna*. Other characters such as the massive scolex form, the heteromorphous metabasal armature, and the testis sizes are similar in both species. The type material of *H. heteromorphi* needs to be re-examined to confirm the differences between the species.

## ***Mixonybelinia southwelli*** (Palm & Walter, 1999)

*Material examined*

From *Makaira indica* (Cuvier, 1832): 1 postlarva, Cape Bowling Green, Queensland, coll. P. Speare, 18.ix.1987 (QM G 218061).

From *Chaerodon venustus* (DeVis, 1885): 1 postlarva, Heron Island, Queensland, coll. R. Bray, 30.i.1991 (QM G 218062).

*Description*

SL = 2000, 1550; SW = 1050, 690; pbo = 1030, 890; pv = 850, 660; pb = 440, 590; ppb = 40; vel = 450, 220; app = 670, 270; BL = 411 (400–425), 548 (520–580); BW = 153 (140–165), 153 (140–170); BR = 2.7:1, 3.6:1; SP = 2.3:1.9:1, 1.5:1.1:1. Tentacle sheaths spirally coiled; TSW = 55–60, 50–60. Prebulbar organs absent, muscular rings around the basal part of tentacle sheaths not seen; retractor muscles originate in basal part of bulbs, tentacular swelling absent; TW basal = 50.0–55.0, 47.5–55.0, TW metabasal = 35–47, 30–35. Armature homeoacanthous, heteromorphous; characteristic basal armature consisting of about 14–16 rows. Antibothridial metabasal hooks massive, rosethorn-shaped, L = 15.0–17.5, 15.0–16.3, B = 13.7–15.0, 15.0–17.5; bothridial hooks more slender and slightly curved with stout base, L = 18.7–20.0, 17.5–20.0, B = 11.3–12.5, 11.3–13.8. Basal armature homeomorphous, hooks falciform with stout base and strongly recurved tip, L = 15.0–22.5, 18.8–21.3; B = 7.5–8.7, 7.0–8.0; hsr basal = 6–7, hsr metabasal = 5–6.

*Remarks*

The postlarva from *Chaerodon venustus*, collected at Heron Island, is similar in scolex size and proportions, armature pattern and hook sizes to those described for *M. southwelli* by Palm and Walter (1999). Differences in scolex measurements of the specimen from *Makaira indica* are probably due to the shrunken condition of that specimen. The change in armature pattern from falciform basal hooks to heteromorphous rosethorn-shaped metabasal hooks is characteristic for *M. southwelli*. The distribution of the species is extended to eastern Australian waters, and *Makaira indica* and *Chaerodon venustus* represent new hosts for the species.

## Genus *Kotorella* Euzet & Radujkovic, 1989

**Kotorella pronosoma** (Stossich, 1901)
(Fig. 54)

*Material examined*

From *Dasyatis fluviorum* Ogilby, 1908: 2 adults, Moreton Bay, Queensland, coll. S. Butler, 26.ix.1980 (QM G 218063–218064).

*Description*

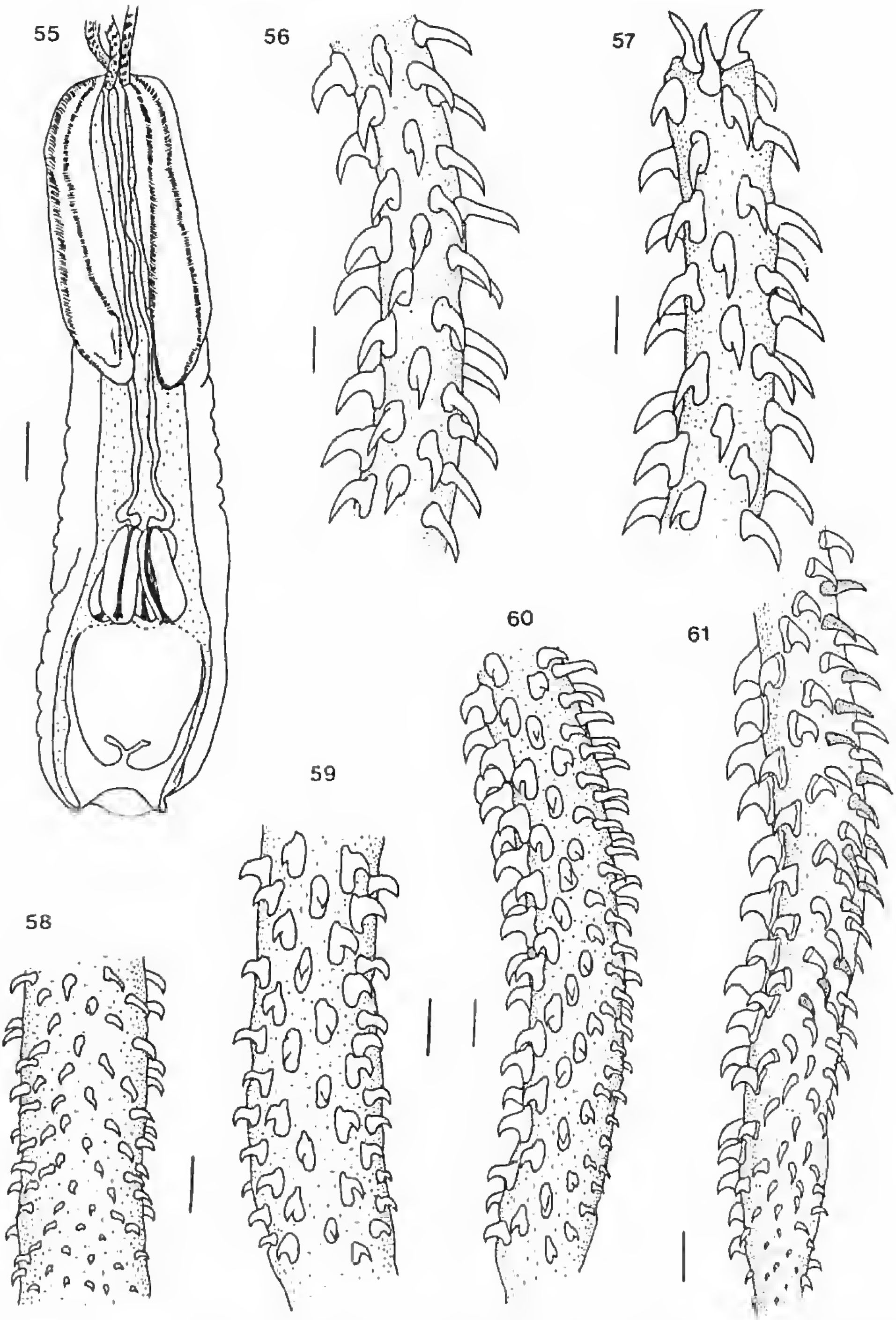
SL = 570, 660; SW = 200, 200; pbo = 400, 390; pv = 385, 510; pb = 80, 85; vel = 110, 80; BL = 71 (70–73), 78 (71–88); BW = 39.4 (37.5–40.0), 40.0 (35.3–45.0); BR = 1.8:1, 2.0:1; SP = 5.0:4.8:1, 4.6:6.0:1. TW basal = 17.5, 22.5. Basal tentacular swelling absent. Tentacle sheaths straight; TSW = 11.3–15.0, 5.5–15.0. Prebulbar organs and muscular rings around basal part of tentacle sheaths absent; retractor muscles originate in basal part of bulbs. Tentacular armature homeoacanthous, heteromorphous; basal hooks on bothridial surface L = 6.3–7.5, 6.3–7.5, B = 5.0–6.0, 5.0–6.0, smallest hooks on antibothridial surface L = 2, increasing in size towards metabasal region. Small, incomplete worms to 15 mm long, maximum width 570; 90 segments. Strobila acraspedote; pre-mature segments 30 x 110 – 260 x 360, mature segments longer than wide or wider than long, 480 x 430 to 550 x 620 (Fig. 54). In second specimen, mature segments 500 x 440 to 550 x 650, and pre-gravid (with some eggs) segments 320 x 710 to 750 x 620. Genital pores submarginal, 210 from anterior margin; alternate irregularly. Cirrus sac elongate, 150–250 x 30–60 (n = 5) in mature segments, length:width ratio 4.4:1 (4.0–5.0:1); cirrus unarmed; internal and external seminal vesicles absent. Vas deferens in large coils, extends to midline of segment, then posteriorly towards female genital complex. Testes 86 (81–100) in number, 45–85 in size (central), smallest testes 20–50 (peripheral), distributed in single layer, confluent posterior and anterior to ovary. Ovary median, ovarian lobes 110–200 x 100–150; Mehlis' gland small, situated between ovarian lobes. No vitelline follicles in centre of the segment, follicles 33 (25–45) in diameter. No uterus observed, spherical eggs appear in parenchyma, egg diameter 22 (15–40).

*Remarks*

The morphology of *Kotorella pronosoma* (Stossich, 1901) is summarised by Euzet and Radujkovic (1989), Palm and Walter (1999) and Palm and Overstreet (2000). The present specimens from Moreton Bay correspond in scolex size and proportions as well as in the tentacular armature with the other described specimens. The sole difference noted was in testis number which exceeded 80 per segment in the specimens described. The species has previously been found in rays such as *Aetobatus narinari* (Euphrasen, 1790 ) (see Palm & Overstreet 2000), *Himantura imbricata* (Bloch & Schneider, 1801), *Rhynchobatus djiddensis* (see Shipley & Hornell 1906; Palm & Walter 1999) and *Dasyatis pastinaca* (Linnaeus, 1758) (see Euzet & Radujkovic 1989; Palm & Walter 2000). *Dasyatis fluviorum* represents a new host record, and the range of distribution is extended to eastern Australian waters. The present finding suggests a cosmopolitan distribution for the species. Previously, the nearest known occurrence of this cestode to Australia was from the Java Sea under the name *Nybelinia narinari* (MacCallum, 1917), now a synonym of *Kotorella pronosoma* (see Palm & Overstreet 2000).

## *Kotorelliella* gen. nov.

*Diagnosis*: Tentacles elongate, slender; retractor muscle originates at base of bulbs. Metabasal tentacular armature homeoacanthous, heteromorphous; hooks on bothridial surface uncinate becoming slender towards antibothridial surface. Basal hooks heteromorphous; characteristic basal armature present, arranged in a heteroacanthous atypica pattern with




FIGURES 55–61. *Kotorelliella jonesi* gen. et sp. nov. from *Taeniura lymma*. Holotype, QM G 218065. **55**. Scolex. **56–57**. Metabasal and apical armature, external view. **58**. Basal armature, bothridial view. **59**. Basal armature, antibothridial view. **60–61**. Basal towards metabasal armature, external view. Note the interpolated hooks as in Fig. 61. Scale bars: Figure 55, 150 µm; Figures 56–61, 10 µm.

interspersed hooks on the antibothridial tentacle surface. Hooks solid. Strobila unknown.

Type-species: *Ko. jonesi* sp. nov.

***Kotorelliella jonesi*** sp. nov.
(Figs 55–61)

*Types*

Holotype, 1 postlarva from the spiral valve of *Taeniura lymma* (Forsskål, 1775), Heron Island, Queensland, coll. I. Beveridge & M. K. Jones, 11.vii.1998 (QM G 218065).

*Material examined*

Holotype.

*Description*

Scolex compact, 4 elongated bothridia, with hook-like microtriches along bothridial borders. Posterior margins of bothridia free, not fused with peduncle. SL = 1910 (Fig. 55); SW = 390; pbo = 800; pv = 1140; pb = 260; vel = 460; BL = 259 (250–265); BW = 82.5 (80–85); BR = 3.1:1; SP = 3.1:4.4:1. Tentacles long and slender; TW basal and metabasal = 21.2–23.8; TW apical = 17.5–20; basal tentacular swelling absent. Tentacle sheaths straight; TSW = 15.0–17.7. Prebulbar organs and muscular rings around basal part of tentacle sheaths absent; retractor muscles originate in basal part of bulbs. Metabasal (Fig. 56) and apical (Fig. 57) armature homeoacanthous, heteromorphous. Rosethorn-shaped hooks with anterior extension of base cover bothridial tentacle surface (L = 13.5–15.0, B = 7.5–10.0); antibothridial surface with slender spiniform hooks, recurved at tip (L = 15.0–17.5, B = 5.0–6.3); hooks decrease in size towards apical armature; hook shape remains constant (bothridial: L = 11.3–13.7, B = 10.0–11.2; antibothridial: L = 12.5–13.7, B = 4.5–5.5). Basal armature (Figs 58–61) with additional hooks interspersed on antibothridial surface; hook pattern heteroacanthous atypica, consisting of about 5 rows of hooks on bothridial (Fig. 59) and 9–10 rows on antibothridial (Fig. 58) tentacle surface; basal hooks on bothridial surface L = 6.3–10.0, B = 6.3–8.8, on antibothridial surface L = 2.0–10.0, B = 1.5–3.8, continuously increasing in size from base of tentacle towards metabasal armature (Figs 60–61).

*Remarks*

The holotype of *Kotorelliella jonesi* gen. et sp. nov. has a unique form of armature within the Tentaculariidae, changing from a homeoacanthous, heteromorphous hook pattern with rosethorn-shaped hooks in the metabasal armature to a heteroacanthous atypica hook pattern in the basal armature. The size of hooks in the basal and apical regions is smaller than in the metabasal region.

On the basis of the scolex morphology, *Ko. jonesi* sp. nov. appears to be similar to *Kotorella pronosoma*. Both species have an elongated scolex, four elongated and slender bothridia with free margins, and short oval bulbs. In both species, the metabasal armature is heteromorphous, with hooks changing from uncinate on the bothridial surface to elongate on the antibothridial surface. Both species have a band of hook-like microtriches along bothridial borders, which are clearly visible using light microscopy. Such a microthrix pattern is characteristic for tentaculariid trypanorhynch cestodes.

The basal armature of *K. pronosoma* is homeoacanthous, but that of *Ko. jonesi* sp. nov. is unusual, having additional hooks interspersed between the oblique spirals of hooks. Thus, the basal tentacular armature is heteroacanthous atypica. The basal region is homeoacanthous in *Nybelinia*, *Heteronybelinia* and *Mixonybelinia*, but in *Tentacularia*, the bothridial surfaces of the tentacle have extra rows of small hooks (see Beveridge & Campbell 1996). The unique feature of the tentacular armature suggests that the erection of a new genus is justified, even though it is known only from the larval stage.

The new species was named after one of the collectors, Dr M. K. Jones, from the Centre for Microscopy and Microanalysis, University of Queensland, Australia.

**Unidentified material**

The following additional material, some of which represent new host records, was examined but could not be assigned to a species:

*Nybelinia* sp. from the spiral valve of *Rhynchobatus djiddensis*, Flat Top Island, Queensland, coll. B. G. Robertson, 25.x.1985 (SAM AHC 28325).

*Nybelinia* sp. from the spiral valve of *Notorhynchus cepedianus* (Péron, 1807), south coast Kangaroo Island, South Australia, coll. B. G. Robertson, 10.ii.1985 (SAM AHC 28327).

*Nybelinia* sp. from the stomach of *Notorhynchus cepedianus*, Young Rocks, Kangaroo Island, South Australia, coll. B. G.

Robertson, 23.v.1985 (SAM AHC 21354, 28328)

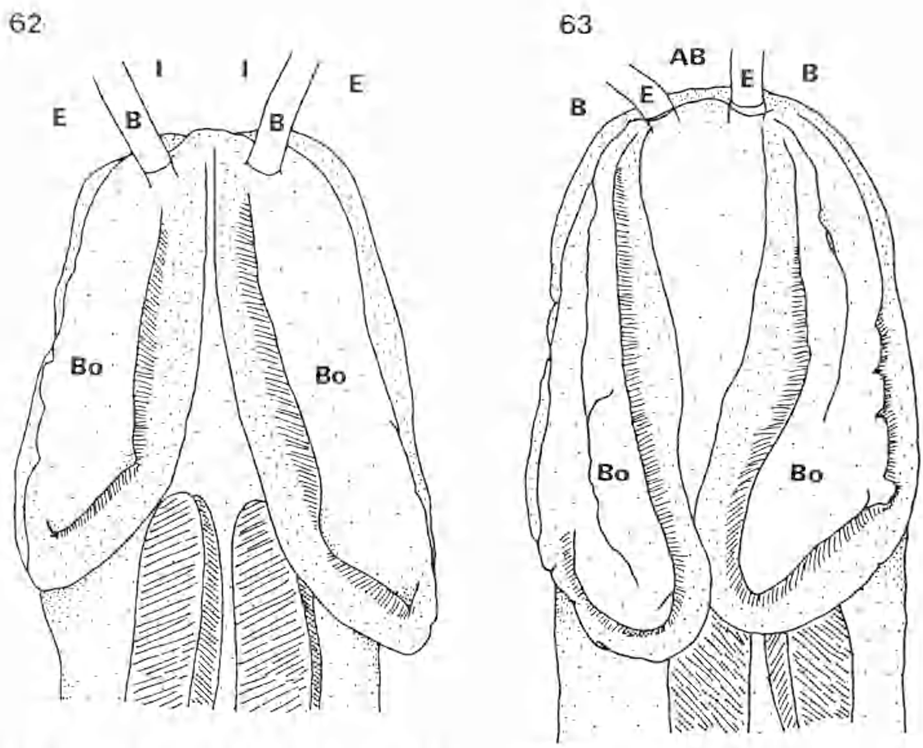
*Heteronybelinia* sp. from the spiral valve of *Carcharhinus amblyrhynchoides*, Tommy Cut Mouth, Northern Territory, coll. B. G. Robertson, 19.ix.1986 (SAM AHC 18326).

## Discussion

The present study provides an overview for the first time of the tentaculariid trypanorhynch fauna from the Australian region. Three new species are added to the genus *Nybelinia*, two to *Heteronybelinia* and one to *Mixonybelinia*, with the latter two genera, as well as *Kotorella*, reported from the Australian region for the first time. In addition, a new genus *Kotorelliella* gen. nov., is erected, which is characterised by a homeoacanthous, heteromorphous metabasal armature and a heteroacanthous basal armature. Other features such as the elongated, widely spaced bothridia and the short bulbs appear similar to *Kotorella*.

The tentaculariid trypanorhynch fauna in Australian waters is relatively species rich with 22 (48 %) of the total of 46 known species occurring in these waters. Several of the new species may be endemic. However, the distribution of many species is still imperfectly known and a number of species previously thought to be endemic to a specific region have subsequently proven to be cosmopolitan (Palm et al. 1997; Palm 1999; Palm & Walter 1999, 2000). Reasons for broad distributions within tentaculariid trypanorhynchs may relate to life-cycle patterns, including widely distributed fish intermediate and elasmobranch definitive hosts. Another reason might be the low host specificity of the parasites, particularly in the intermediate host (Palm et al. 1997; Palm & Walter 2000).

It is difficult to clearly distinguish between




FIGURES 62–63. Schematic drawing of scolex of *Heteronybelinia pseudorobusta* sp. nov. from *Lepidotrigla modesta*, illustrating the arrangement of the different tentacle surfaces within tentaculariid trypanorhynchs. **62**. View from bothridial surface, with bothridial borders merging at the apex of the scolex. **63**. View from external surface, with bothridial borders widely spaced. Abbreviations, AB = antibothridial view, B = bothridial view, Bo = bothridia, E = external view, I = internal view.

some tentaculariid species solely on the basis of the tentacular armature (eg *N. strongyla*), and additional taxonomic characters are required. To date, the strobilae of only a few tentaculariid species have been described in detail. The present study demonstrates that, apart from the number and size of different genital structures, the cirrus sac length:width ratio might be a useful character as, for example, in *H. australis* sp. nov. and *N. hemipristis* sp. nov. The position of the anterior end of the cirrus sac and the distance of the genital pore from the anterior end of the segment, as well as the number of layers of testis, whether the testes are confluent posterior to the ovary, and the number of testes anterior to the cirrus sac appear to be useful taxonomic features. Further species descriptions are needed to show whether or not these characters are variable, as is observed in a number of scolex characters, or whether they can be used more widely in tentaculariid systematics.

During this and previous studies, it became evident that the descriptions of the different tentacular surfaces of trypanorhynch cestodes used by Dollfus (1942) and Campbell and Beveridge (1994) may be difficult to apply to larval tentaculariids. In many cases it was hard to identify the various tentacle surfaces. For a better understanding of the position of the four tentacles within tentaculariid trypanorhynchs, the following two schematic illustrations are given (Figs 62, 63) as they may help to standardise the orientation of the different tentacle surfaces within tentaculariid trypanorhynchs. The determination of tentacle orientation is based upon whether the bothridial borders merge at the apex of the scolex (Fig. 62) or whether they are widely spaced (Fig. 63). The former figure shows the bothridial and the latter the external view of the tentacle surfaces.

The description of *Kotorelliella jonesi* gen. et sp. nov. is of particular interest since its armature comprises both homeomorphous and heteromorphous components (Campbell & Beveridge 1994; Palm 1995, 1997). The species seems to be closely related to *Kotorella pronosoma*, which has a similar scolex morphology and metabasal armature. Both species have characteristic microtriches along the bothridial borders, which appear similar to those of *Tentacularia coryphaenae* and species of *Nybelinia* (see Palm & Overstreet 2000). Although Beveridge et al. (1999) could not align *Kotorella* with the other tentaculariid genera using cladistic analyses, we consider that *Kotorella pronosoma* and *Kotorelliella jonesi* belong to the Tentaculariidae since they possess a homeoacanthous metabasal armature and, more importantly, bands of hook-like microtriches along the bothridial borders. The latter character has as yet only been described for tentaculariid trypanorhynchs.

Following the classification of Dollfus (1942), only the metabasal armature is considered in classifying the tentacular armature. However, in more recent classifications, trypanorhynchs with a distinct basal armature such as *Mixodigma leptaleum* Dailey & Vogelbein, 1974, *Paroncomegas araya* (Woodland, 1934) and *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997) have been placed in distinctive genera based in part on the basal armature (Campbell & Beveridge 1994; Campbell et al. 1999; Palm 1999). *Kotorelliella jonesi* has thus been placed in a new genus. Interestingly, *K. jonesi* represents a transition from homeoacanthous towards heteroacanthous armature as suggested by Campbell and Beveridge (1994, p. 57, lines 7–11).

In summary, tentaculariid trypanorhynchs show considerable morphological variability, as can be seen by differences in scolex morphology between the genera *Nybelinia*, *Heteronybelinia* and *Mixonybelinia*, and between *Kotorella* and *Kotorelliella*. The tentacular armature also differs between the species, varying from homeoacanthous and homeomorphous (*Nybelinia*, *Mixonybelinia*) to homeoacanthous and heteromorphous (*Heteronybelinia*, *Kotorella*, *Mixonybelinia*) patterns. *Kotorelliella* has a homeoacanthous metabasal and a heteroacanthous basal hook pattern. Additional methods, such as molecular genetic studies, might help to resolve not only species relationships but also the phylogenetic relationships of the species and species groups within this large trypanorhynch family.

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